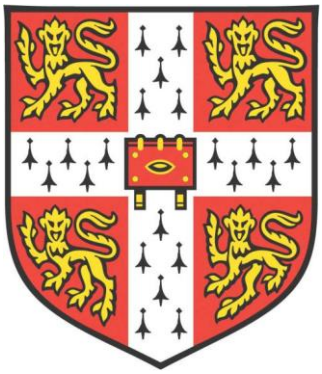
Intraspecific variation in environmental and geographic space use: insights from individual movement data



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Author's Declaration

This dissertation is the result of my own work and includes nothing which is the outcome of work done in collaboration except as declared in the Preface and specified in the text.

It is not substantially the same as any that I have submitted, or, is being concurrently submitted for a degree or diploma or other qualification at the University of Cambridge or any other University or similar institution except as specified in the text.

I further state that no substantial part of my dissertation has already been submitted, or, is being concurrently submitted for any such degree, diploma or other qualification at the University of Cambridge or any other University or similar institution.

The main text does not exceed the prescribed word limit for the relevant Degree Committee (School of Biology).

Summary

Species' ranges arise from the interplay between environmental preferences, biotic and abiotic environmental conditions, and accessibility. Understanding of – and predictive models on – species distributions often build from the assumption that these factors apply homogenously within each species, but there is growing evidence for individual variation. Here, I use movement data to investigate individual-level decisions and compromises regarding the different costs and benefits influencing individuals' geographic locations, and the species-level spatial patterns that emerge from these.

I first developed a new method that uses tracking data to quantify individual specialisation in geographic space (site fidelity) or in environmental space (environmental specialisation). Applying it to two species of albatrosses, I found evidence of site fidelity but weak environmental specialisation. My results have implications for how limited research efforts are best-targeted: if animals are generalists, effort are best spent by understanding in depth individual patterns, i.e., better to track fewer individuals for long periods of time; whereas if animals tend to be specialists, efforts should be dedicated to tracking as many individuals as possible, even if for shorter periods.

I then investigated individual migratory strategies and their drivers in nine North American bird species, using ringing/recovery data. I found latitudinal redistribution of individuals within the breeding and non-breeding ranges that generally did not follow textbook patterns ('chain migration' or 'leapfrog migration'). Migratory individuals tend to trade off the benefits of migration (better tracking of climatic niche; better access to resources) and its costs (increasing with migratory distance). I found that birds are more likely to remain as residents in areas with warmer winter temperatures, higher summer resource surpluses and higher human population densities (presumably because of a buffering effect of urban areas).

Overall, my results highlight the importance of considering individual variation to understanding the ecological processes underpinning species' spatial patterns.

Acknowledgements

Like the birds in this thesis, I spent my PhD migrating between two seasonal ranges: one in Cambridge, in the Zoology Department and one in Montpellier, at the Centre d'Ecologie Fonctionnelle et Evolutive. My general thanks go to all the people I have met in these two amazing places and who have made this thesis possible and enjoyable.

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The incredibly stimulating environments I was working in also highly helped me fledge as a scientist. Both the Zoology Department and the CEFE are amazing places to work at: places with opportunities to discuss research – be it the Stats Club in the David Attenborough Building, the Student Conference for Conservation Science in Cambridge (a yearly highlight of my time in Cambridge), the journées DPB, the JCM or the student seminars at the CEFE –, places with very smart people to interact with and exciting seminars to attend.

Not only stimulating, my working environment has also been incredibly friendly. For this I would like to thank all the amazing people whose path crossed mine in my two labs in these last years: all the people in the (extended) Evolutionary Ecology group: Marius, Tommy, Ana, Dave, Max, Veronika, Riva, Freddie, Robert, Stephen, Mario, Anahit, Maanasa, Ana… ; all my Happy Hour companions at the Zoology Department; all my colleagues at the CEFE: Ana, Anne, Jean-Louis, Paul, Simon, Simon, Marius, Sophie, Sophie, Louise, Guillaume, Marie, Adrien, Noémie, Eva, Sarah, Fabien, Carole, Fred, Alice, Clémence, Laeti, Olivier, Gilles, Stpéhane, Fede, Hugo, Nico, Rémi, Adrien, Amémé, Manon, Alexis, Giorgia, Pascal, Julie, Camille, Victor, Agathe, Elodie, Lorelei, Thomas, Laure, Soumaya, Aïssa, Mathias, Matthias, Charlotte, Charlotte, Antoine… Thank you all for creating such a lovely place – and for all the "goûters": like the birds in this thesis, I understood the importance of "resource surpluses"!

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Although they have been incredibly stimulating, it would probably be lying not to say that these PhD years have also been hard. So I would like to dedicate this PhD to the people who supported me in times of self-doubt and helped me bounce back – there have been many, but I am particularly grateful to Laeti, Nico, Veronika, Elodie, Maanasa and Rémi.

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1. General introduction

1.1. Drivers of species distributions

Species ranges represent the delimitation of where the species can be found. They are usually described using broad-scale sampling from a large number of observations. There can be considerable within-taxon variation in the sizes of species ranges: going from endemic species (very restricted range, e.g. the Sulawesi masked owl, *Tyto rosenbergii*, endemic to a few islands in Indonesia, IUCN 2018) to widespread species (e.g. the Common barn-owl, *Tyto alba*, found on all continents apart from Antarctica). The size of the range can inform us about the risk of extinction of a species, and is therefore used to define conservation status (IUCN Red List, IUCN 2012). The distribution of species can also help identify important areas for conservation (e.g. identifying areas with high species richness), as well as to monitor the impacts of global changes on species or the outcome of introductions (of alien species) or re-introductions.

But what are the factors that influence species distributions? First, species are found where the abiotic environment is favourable for them. This mainly refers to climatic conditions: precipitation, temperature, etc. Being in an unfavourable environment should be costly (e.g. cost of thermoregulation in cold environments, Porter and Kearney 2009). The abiotic environment that is favourable for a species is commonly referred to as the 'Grinellian niche' (Soberón 2007), and variables characterising that environment are called 'scenopoetic variables' (Hutchinson 1978). However, it should be noted that contrary to the way the Grinellian niche is traditionally seen, the distinction between favourable and unfavourable environment does not have to be discrete, but can rather be seen as a gradient (with optimal conditions and a range of suitable – although not as good – conditions around the optimum). In that framework, populations benefit from being in more favourable environments (i.e. the population growth rate is higher in such environments, mainly through increased individual survival and/or reproduction).

Second, species are influenced by biotic factors: resources, competitors, predators, etc. For example, higher amounts of available resources (i.e. higher levels of resources and/or lower amounts of competitors) make areas more suitable to the studied species. The biotic factors allowing a species to maintain itself in a certain area are commonly referred to as the 'Eltonian niche' (Soberón 2007) and the variables representing such factors are the 'bionomic variables' defined by Hutchinson (1978). In a similar way as above, these biotic factors need not be seen

as creating a dichotomy between conditions in which a species can live and conditions in which it cannot (e.g. because of the presence/absence of certain prey species), but can also be seen as continuum of more to less favourable conditions (e.g. related to the amount of resources available). In that framework, populations benefit more by being distributed in areas with more favourable biotic conditions.

Last, species are found in areas that were historically accessible to them. The success of invasive species outside their native range demonstrates the existence of areas where species could have thrived had they been able to reach them (Sax et al. 2007). Although the traditional view is a dichotomy between accessible and non-accessible areas, we can also consider it as a gradient of more or less accessible areas. Indeed, if some barriers are more or less impassable (e.g. rivers, lakes or oceans for terrestrial species, currents for oceanic species), in many cases there are continuous costs to accessibility (e.g. energetic costs of flying long distances for birds, but also mortality risks associated with crossing unfavourable habitats – i.e. habitats with increased risk of predation, with low amount of available resources, etc.).

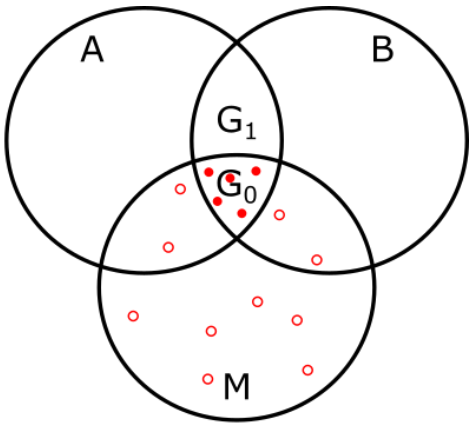

Figure 1.1: A BAM diagram*, adapted from Soberón and Nakamura (2009). A: regions where the scenopoetic conditions of the 'potential niche' occur, B: regions where the biotic conditions would allow the existence of viable populations (determined mainly by Eltonian factors), M: region that has been accessible to dispersal by the species over some relevant time interval, G0 (A ∩ B ∩ M): area actually occupied by the species, G1 (A ∩ B ∩ non(M)): potentially invisible area (correction abiotic and biotic conditions but outside reach).*

BAM (biotic, abiotic, movement) diagrams (Soberón and Nakamura (2009); Fig.1) are a simplified representation of these costs/benefits. The latter relate species distributions with their niche, by considering that species should be found at the geographical intersection between A – the regions where the scenopoetic conditions under which the population growth rate of the species would be positive actually exist at a given time, B – the regions where the biotic conditions would allow the existence of viable populations, and M – the regions that are accessible to the species. However, this view is rather discrete (favourable vs. unfavourable regions), while where species are found is more likely to represent compromises between the above-mentioned costs and benefits.

To describe a species niche, the usual approach is to use its distribution in geographical space and build species distribution models (Austin 2007). For this purpose, the presence (and potentially absence) of the species is recorded at different locations, and statistically related to local environmental conditions. The resulting understanding of the relationship between the species and its environment can in turn be used to make predictions on where the species will be found (Elith and Leathwick 2009), either in space (in non-sampled areas) or in time (e.g. in response to climate change).

1.2. An individual-level perspective

Species distributions can be described at different scales. In many cases (e.g. the maps produced by the IUCN, IUCN 2018), a coarse scale is used, via the 'extent of occurrence' ("the area within the outer most limits to the occurrence of a species", Gaston 2003). However, if we zoomed in, not all areas in the extent of occurrence would be occupied by the species. The 'area of occupancy' describes where the species is actually found, and is usually much patchier than the extent of occurrence as favourable habitats are usually discontinuous: this represents different populations. If we keep zooming in, individuals are the ultimate relevant unit: they are the ones making the decisions from which the species patterns emerge.

The costs and benefits mentioned above translate at the individual level: individuals need to be in the abiotic environment to which they are adapted to be able to survive and reproduce effectively; they face energetic and mortality costs when trying to access remote places (Wikelski et al. 2003, Newton 2008); they benefit by having access to more resources. There can however be differences between individuals in the values of these costs/benefits, or in the strategies adopted to compromise such costs/benefits.

When they affect environmental preferences, these differences between individuals translate into specialisation. In practice, the situation is likely to fall somewhere between the two following scenarios: 1) the population/species is composed of individuals that have the same broad niche distribution (generalist individuals, Figure 1.2A); 2) the niche distribution of the population/species is composed of individuals having different narrow niche distributions (specialist individuals relative to the population = "individual specialisation", Figure 1.2B). The degree of intraspecific/intra-population niche variation can have various consequences (see Bolnick et al. 2003 for a review).

From an ecological point of view, individual specialisation tends to occur when intra-specific competition is high (Araújo et al. 2011), so individual specialisation can be seen as a way to dampen the effects of such competition. Intraspecific/intra-population niche variations also affect the exposure of different parts of the population to predators – mostly through differences in foraging habitats – and to parasites – potentially also through the ingestion of different preys (Reimchen 1980, Reimchen and Nosil 2001). This is likely to influence population dynamics, through an increased scope for frequency-dependent effect (e.g. by reducing the number of potential hosts in host-parasite systems, or by reducing the number of individuals an individual is competing with).

From an evolutionary point of view, intraspecific/intra-population niche variation can make different selective pressures act on different individuals within the same population. Fitness differences can exist between generalists and specialists (probably mostly because of frequency-dependent competition, e.g. Golet et al. 2000) or between different types of specialists (probably mostly because of different predation risks and prey energetic value, e.g. Annett and Pierotti 1999). In the case when specialists have a higher fitness than generalists, there can be disruptive selection, a phenomenon that can allow the maintenance of polymorphisms (Wilson and Turelli 1986) or even favour reproductive isolation, potentially leading to sympatric speciation (Dieckmann and Doebeli 1999).

From a conservation perspective, there are consequences both for species' resilience to threats and for our own understanding of species requirements. First, intra-population niche variation may help to buffer against the loss of particular habitats or resources. Although specialist individuals may lack the potential flexibility for responding to environmental change (Bolnick et al. 2002), a population made of specialist individuals (i.e. high intra-population niche variation) may possess the genetic variation for such adaptation on a longer time scale (Bolnick et al. 2003). Second, individual specialists may suffer from attempts at protecting a species'

resources by targeting some average resource for the population (Bolnick et al. 2003), and the degree of intraspecific/intra-population niche variation influences how many individuals need to be studied in order to get representative view of the population/species.

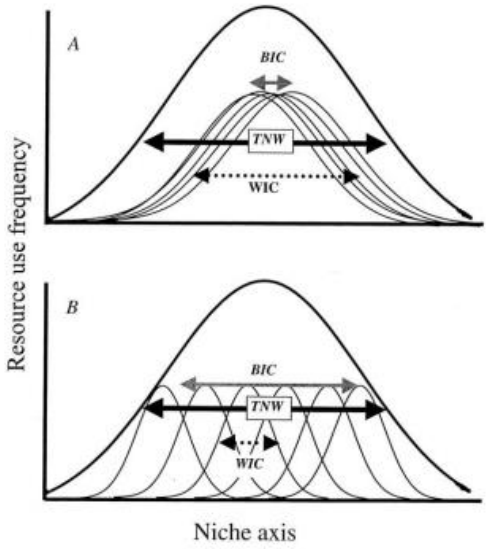

Figure 1.2 *(extracted from Bolnick et al. 2003):* ***A schematic diagram of how individuals can subdivide the population's niche*** *(thick line). TNW: total niche width, BIC: between-individual component and WIC: within-individual component*

A difficulty with the study of intra-specific differences is that, in order to build the preference distribution of an individual along a particular axis of interest, repetitions of the individual's choices on that axis are needed. This can be easily observed for prey selection, as each meal is potentially an independent replicate (see Bolnick et al. 2003, Araújo et al. 2011, Ceia and Ramos 2015 for reviews). However, understanding intra-specific variation in site and habitat preferences is more complex, as it is hard to know whether individuals are found where they are because of chance or because of an active choice. As a solution, individual movement data from species that can be very mobile can be used as a 'natural experiment' to understand individual preferences, as long-distance movements can be seen as a series of repeated choices (on where to go next, at which costs, under which conditions, etc.). Using that approach, a number of studies have provided evidence for intraspecific differences in geographical strategies, particularly related to bird migration (to migrate or not, Singh et al. 2012, Perez et

al. 2014; or in migration routes, Phillips et al. 2005, Gschweng et al. 2008, Catry et al. 2011, Vardanis et al. 2011, Dias et al. 2013, McFarlane Tranquilla et al. 2014) but also foraging site fidelity (e.g. Wakefield et al. 2015).

However, although individuals follow continuous paths, the information that we can gather is always discrete and therefore incomplete. There are different techniques to obtain information on where individuals went, and they all present a series of advantages/ disadvantages related with the quality/precision of the reconstruction of the individual movement, as well as the number of individuals than can be studied (because of various costs and the practicality of fitting the device/retrieving information). With the development of large-scale schemes (e.g. EURING, du Feu et al. 2016; Motus Wildlife Tracking System, https://motus.org/) and initiatives to share data (e.g. Movebank, www.movebank.org; Seabird Tracking Database, http://www.seabirdtracking.org/) and as loggers become lighter, cheaper and more performant (see Ponchon et al. 2013 for a review), more and more movement data are becoming available, providing us with the opportunity to better detect and understand the above-mentioned intraspecific variations.

In particular, here I focus on two types of individual movement strategies: foraging strategies and migratory strategies. Understanding individual space use is important to be able to design protected areas that efficiently target this space used. This is particularly true at the scale at which individuals forage, as understanding how similarly individuals behave will influence, for instance, whether targeting an average environment for the whole species would be efficient. At the spatial scale of migratory strategies, understanding the individual drivers of such migrations is also particularly important in a context in which migratory species are declining. Macroecological studies have shown what some of the drivers of migration are at the species level, mainly in terms of climatic niche benefits and access to resources (see Somveille et al. (2015); and Chapters 5 and 6 for more detailed reviews). However, taking an intraspecific approach would allow a much finer view of what drives migratory decisions, which would in turn help us predict what might happen for migrations in the future (e.g. with climate change or with changes in the distribution of resources). Finally, an intra-specific understanding of migration can help us understand which breeding and non-breeding areas are connected, which can potentially have consequences for the spread of infectious diseases (either increasing the risk of infection by connecting disjoint areas, or reducing it by allowing individuals to escape contaminated areas, Altizer et al. 2011)".

1.3. Objectives

In this thesis, I use individual movement data to investigate individual-level decisions/compromises regarding the different costs and benefits influencing their geographic locations. I try to understand how species-level spatial patterns emerge from these individual decisions.

Throughout the thesis, I focus on birds. Their ability to fly allows them to move long distances, making them a good study system. I use two types of bird movement data: ringing data – providing very few data points per individual, with a low spatial resolution but covering many individuals at a large spatial scale – and tracking data (using Platform Terminal Transmitters) – providing many data points per individual, but only for a few individuals.

1.4. Thesis outline

A first step when trying to understand how species-level patterns emerge from individual decision is to be able to detect and quantify individual differences in space use. Individual differences can emerge in geographical space, but also in environmental space (i.e. individual specialisation). For this reason, I reviewed existing methods used to detect and quantify individual specialisation using diet and movement data of marine predators and present them in chapter 2.

Following this review, I developed a new method to quantify individual specialisation using tracking data. In chapter 3, I present and apply this method to two seabird species, Black-browed albatrosses *Thalassarche melanophris* and Grey-headed albatrosses *Thalassarche chrysostoma*, equipped with Platform Terminal Transmitters in South Georgia.

In Chapters 4 to 6, I extend the study of individual differences to all three costs/benefits axes discussed above using a large scale ringing/recovery dataset on nine species of partially migratory North American passerines and near passerines. In Chapter 4, I develop a method to characterise within-species migratory patterns, and to formally identify leapfrog and chain migration, as opposed to a random redistribution of individuals from one season to the next.

In Chapter 5, I test hypotheses about drivers of migration at the individual level and find that migration allows individuals to track better their niche and to increase their access to resources compared with if they had stayed. I find that these advantages are traded off against the cost of migratory distance. My results also suggest that when other options are considered, individuals

actually do not perform as well as they could. My results indicate that emphasis is put on minimising migratory distance rather than maximising the above-mentioned benefits.

In Chapter 6, I investigate what drives the choice of individuals to migrate or not. I find that individuals are more likely to remain residents in more favourable conditions (warmer winter climate and higher surplus of resources in summer compared than winter). For some species, high human population density also increases the probability of individuals to remain resident.

Finally, in Chapter 7, I present an overall discussion of this thesis and perspectives for future research.

2. Methods for detecting and quantifying individual specialisation in movement and foraging strategies of marine predators

2.1. Abstract[1]

There is increasing realisation that individuals in many animal populations differ substantially in resource, space or habitat use. Differences that cannot be attributed to any a priori way of classifying individuals (i.e. age, sex and other group effects) are often termed "individual specialisation". The aim of this chapter is to assess the most common approaches for detecting and quantifying individual specialisation and consistencies in foraging behaviour, movement patterns and diet of marine predators using three types of data: conventional diet, stable isotope ratios and tracking data. Methods using conventional diet data rely on a comparison between the proportions of each dietary source in the total diet and in the diet of individuals, or analyses of the statistical distribution of a prey metric (e.g. size); the latter often involves comparing ratios of individual and population variance. Approaches frequently used to analyse stable isotope or tracking data reduced to one dimension (trip characteristics, e.g. maximum trip distance or latitude/longitude at certain landmarks), include pair difference tests and repeatability analysis. Finally, various spatial analyses are applied to other types of tracking data (e.g. distances between centroids of distributions or migratory routes, or overlap between distributions), and to compare habitat use. We discuss the advantages and disadvantages of these approaches, issues arising from other effects unrelated to individual specialisation per se (in particular those related to temporal scale) and potential solutions.

[1]This chapter was written jointly with Dr A.P.B Carneiro and a version of it has been published: Carneiro*****, A., **A.-S. Bonnet-Lebrun***, A. Manica, I. Staniland, and R. Phillips. 2017. Methods for detecting and quantifying individual specialisation in movement and foraging strategies of marine predators. *Marine Ecology Progress Series* 578:151–166. ***authors contributed equally**

2.2. Introduction

Ecologists have often treated conspecific individuals as broadly equivalent, after accounting for age, sex and other group effects (Bolnick et al. 2003, Yamamoto et al. 2014, Wakefield et al. 2015). However, there is increasing realization that individuals in many animal populations differ substantially in resource use ("niche variation"), and the term "individual specialisation" has been used to describe heterogeneity in resource use (Araújo et al. 2011, Patrick et al. 2014, Ceia & Ramos 2015). The extent of niche variation has important implications, including the potential not only to reduce the degree of intra-specific competition, but also to increase individual efficiency in finding and handling food (Cook et al. 2005, Kotzerka et al. 2011, Ceia and Ramos 2015). Moreover, if a wide range of habitats and resources are used, a particular species or population may be better buffered against anthropogenic impacts, as individuals are likely to respond in different ways to changes in the environment (Phillips et al. 2009a, Dias et al. 2011, Masello et al. 2013). Hence, the characterisation of divergent behaviour or strategies may provide important insights into the ecology, evolution, conservation and management of the species (Thiemann et al. 2011, Wakefield et al. 2015, Ramírez et al. 2016).

The interest in individual variation, however, extends far beyond the marine ecology literature, and has evolved independently in several ecological fields, resulting in a fragmented literature with different terminology (Dall et al. 2012). While some researchers have focused on individual niche specialisation (particularly in terms of behavioural traits associated with foraging behaviour and diet choice), others have focused on documenting behavioural syndromes or animal personalities (boldness, aggressiveness, activity, exploration and neophobia), and the division of labour within insect societies (Dall et al. 2012). Although these similar concepts (individual niche specialisation, behavioural syndromes or animal personalities, and the division of labour) are applied in different contexts, they are largely concerned with the same behavioural properties, and each field uses similar statistical methodology for describing individual variation (Cleasby et al. 2015).

Individual specialisation occurs when individuals use a narrow subset of the ecological niche of the population, for reasons not attributed to any *a priori* ways of classifying individuals (Bolnick et al. 2003). Indeed, there are multiple biological reasons to distinguish between phenotypic sex- or age-related variation, and individual-level specialisation (Bolnick et al. 2002). In marine predators, sex differences may arise from the influence of size dimorphism on sex-specific parental roles, inter-sexual competition, foraging and locomotory efficiency (including diving capability), or habitat specialisation (González-Solís et al. 2000, Shaffer et al.

2001, Phillips et al. 2004b, Breed et al. 2006, Quillfeldt et al. 2011, Stauss et al. 2012); these mechanisms are potentially, but not necessarily, different from those generating individual specialisation. Similarly, differences in behaviour are often associated with variation in foraging abilities (i.e. competitive ability) or performance of adults of different ages or experience (Navarro et al. 2010). After accounting for effects of sex and age, other sources of variation among individuals may still exist; this residual variation is what describes individual specialisation. The unexplained within-individual variation is generally assumed to be distributed normally and uniformly between individuals when using this approach (Westneat et al. 2015).

Although a variety of approaches have been used to detect individual specialisation in traits (e.g. diet and foraging behaviour), most approaches rely on contrasting the amount of variation within individuals, with the variation between individuals, using repeatability analysis. A repeatable behaviour will show relatively low within-individual variance compared to between-individual variance (Bell et al. 2009, Potier et al. 2015). Consistently divergent behaviours have also been termed specialisations. The definition of behavioural consistency, however, is not trivial when looking at the statistical methodology, and there is still no universal agreement (but see Cleasby et al. 2015). In the context of specialisation, consistency is to do with variation about a mean value, i.e. the within-individual variation. The within-individual variation needs to be compared to the between-individual variation in order to test for specialisation (to determine a "high" vs. a "low" within-individual variance). Although behavioural consistency can reflect specialisation, it does not necessarily test for individual specialisation as defined here. For example, if groups of individuals (e.g. males vs. females, adults vs. juveniles) differ in their preferences, and if these factors are not accounted for, we might wrongly conclude that there is individual specialisation.

Individual specialisation and behavioural consistency are known to be widespread across a range of taxa and behaviours; they have been demonstrated for a number of species of marine predators in foraging behaviour, migratory routes, dive characteristics, diet, timing of events, activity patterns and habitat choice, and foraging site fidelity during breeding and non-breeding periods (Hoelzel et al. 1989, Staniland et al. 2004, Croxall et al. 2005, Phillips et al. 2005, Sargeant et al. 2005, Phillips et al. 2006, Thiebot et al. 2011, Guilford et al. 2011, Patrick et al. 2014, Yamamoto et al. 2014, Wakefield et al. 2015). Because marine predators forage on highly patchy and more or less predictable food resources at the coarse to mesoscale (tens to hundreds of kilometres) and over days and weeks, the incidence of specialisation is unsurprising

(Weimerskirch 2007, Ceia and Ramos 2015, Wakefield et al. 2015). The recurrent use of similar areas may increase familiarity with feeding conditions, including fine-scale resource availability and distribution (Hamer et al. 2007, Ramírez et al. 2016). Marine predators will often target regions characterised by local physical features or processes, including eddies, frontal systems, upwelling zones and shelf breaks, that increase primary production or serve to aggregate various types of prey (Kappes et al. 2010, Pinet et al. 2011, Louzao et al. 2011, Wakefield et al. 2015, Arthur et al. 2015). Foraging behaviour and diet specialisations may therefore emerge as a result of the spatial and temporal availability and predictability of prey (Woo et al. 2008, Navarro and González-Solis 2009, Sommerfeld et al. 2015, Patrick et al. 2015). Moreover, because marine predators frequently target such productive areas in the breeding and non-breeding seasons, and are central place foragers during breeding, competition may be high and lead to the use of divergent foraging strategies (Estes et al. 2003, Villegas-Amtmann et al. 2008, Patrick et al. 2014, Ceia and Ramos 2015).

Several conventional approaches, such as visual observations, the analysis of pellets, regurgitates or stomach contents, have been used to test for, or to quantify, consistency in diet in marine predators (Votier et al. 2004a, Votier et al. 2004b, Hamer et al. 2007, Maldini et al. 2010). More recently, these approaches have been replaced or supplemented by the use of biologging technology and stable isotope analysis of carbon and nitrogen (Phillips et al. 2005, Furness et al. 2006, Anderson et al. 2009). The aim of this review is to scrutinise the most common methods used to detect and quantify individual specialisation and behavioural consistencies in foraging, movement patterns and diet of marine predators, especially seabirds and marine mammals (Table 2.1). A series of fixed factors unrelated to individual specialisation *per se*, are also discussed briefly, as these need to be taken into account when applying several of the approaches presented here. The review focuses on three types of data: diet assessed using conventional approaches, diet assessed using stable isotopes, and tracking data. In each case, we present the various statistical analyses used to date, providing an overview of the specific advantages and disadvantages.

2.3. Diet using conventional approaches

Many methods are used to study marine predator diet, traditionally involving the collection and analysis of regurgitated prey items and pellets, stomach contents and faeces, direct observations of prey caught or carried by returning adults, or dropped items collected at breeding colonies

(Pierce and Boyle 1991, Barrett et al. 2007, Moreno et al. 2016). The analysis of diet specialisation depends not only on the number of individuals sampled but also, and most importantly, on the number of independent feeding events recorded per individual in order to calculate an index of diet variation (Araújo et al. 2011). Monte Carlo simulations are the only way to do a power analysis, but some prior knowledge of the expected level of variability in a given population is necessary. Although repeated observations over time are required to quantify specialisation correctly, the first studies testing (and rejecting) the null hypothesis that conspecifics share an identical resource distribution were derived from cross-sectional data collected from a population at one specific point in time (Baltz and Morejohn 1977, Lønne and Gabrielsen 1992). Unlike this snapshot approach, longitudinal studies, where sampling at intervals reflects multiple feeding events of the same individual, allow specialisation to be properly quantified at a particular temporal scale.

The simplest approach to detect specialisation is to identify groups of specialists and generalists based on the proportion of each dietary source in the total diet, and assign individuals to these groups (e.g. (Pierotti and Annett 1991, Annett and Pierotti 1999, Oro et al. 2005, Hamer et al. 2007). For example, by observing prey items being delivered to pigeon guillemot *Cepphus columba* chicks for an average of four full days over multiple years, Golet et al. (2000) defined specialists as individuals whose diet contained more than 50 % of a particular item or class of items. Using a higher threshold for the definition of specialist predators, Votier et al. (2004a) categorised great skuas *Stercorarius skua* as specialist fish or bird predators when the contents of regurgitated pellets collected over multiple periods between egg laying and chick fledging comprised 70 % or more of the respective prey, or as generalists when none of the prey items comprised 70 % or more of the diet. When data on diet are not available, behavioural information (such as the proportion of trips associated with fishing boats, and dive depths), or the use of areas where particular prey occur (proportion of time at each feeding site) have been used to assign individuals to different diet groups (Ropert-Coudert et al. 2003, Montevecchi et al. 2009, Masello et al. 2013, Granadeiro et al. 2014, Tyson et al. 2015, Patrick et al. 2015). However, the threshold used for separating specialists and generalists is often arbitrary. Ideally, researchers could deal with this issue by testing the sensitivity of their results to different cut-offs and present that as a supplement. Furthermore, although this approach can be used to infer differences in diet between individuals, which can be interpreted as a form of individual specialisation, it does not allow estimation of its statistical significance.

Table 2.1: Summary of the most common methods used to detect and quantify individual specialisation and behavioural consistencies in foraging, movement patterns and diet of marine predators. WIC: within-individual component, GLMM: generalised linear mixed-effects model, TNW: total niche width, UDOI: utilisation distribution overlap index.

Method	Data type	Example	Reference	Notes
Comparing categories based on percentage of use	Categorical	Prey items	Votier et al. (2004a)	Does not allow statistical testing of the degree of individual consistency
		Habitat types or areas where particular prey occur	Ropert-Coudert et al. (2003)	
Ratios of variance (repeatability)	Continuous variable	Prey trait (e.g. size)	Woo et al. (2008)	Using GLMMs allows the inclusion of fixed effects (not when using Bolnick's WIC/TNW ratio)
		Stable isotope ratios	García-Tarrasón et al. (2015)	
		Trip summary statistics	Wakefield et al. (2015)	
GLMM with random slopes	Response variable and continuous environmental variables	Use/availability locations	-	Resource selection function (habitat selection)
		Foraging trip characteristics, e.g. path straightness	Patrick et al. (2014)	Random slope model
Distances	Spatial data	Between distribution centroids	Navarro & González-Solís (2009)	
		Between migratory routes	Dias et al. (2011)	
Overlaps	Ranges		Orben et al. (2015)	
	Utilisation distributions	In geographical space	Wakefield et al. (2015)	Bhattacharyya's affinity, UDOI, etc.
		In environmental space (each variable at a time)	Wakefield et al. (2015)	Bhattacharyya's affinity, UDOI, etc.

To solve these issues, Bolnick et al. (2002) introduced a framework to quantify and test statistically for individual specialisation in diet that has since been used in a wide range of taxa. By using ratios of variance in a continuous trait measured for each prey item (e.g. prey size), it is possible to estimate how much of the total population variance is explained by differences within vs. between individuals. In practice, the average intra-individual variance ("within-individual component" of the niche, WIC) is calculated, and divided by the sum of the inter-individual variance ("between-individual component", BIC) and the intra-individual variance (WIC + BIC = TNW, the "total niche width"). This index (WIC/TNW) varies from 0 (complete individual specialisation) to 1 (no individual specialisation). Empirical values can be compared with a null model (randomisation of prey items between individuals). This approach can be implemented in the R package RInSp (Zaccarelli et al. 2013). The method can also be extended to discrete data such as the frequency of alternate prey in the diet by using diversity indices as a proxy for variance (Bolnick et al. 2002). Instead of the raw number (or mass) of diet items,

values are transformed into a proportion matrix. Examples of diversity indices applied for this purpose are the Shannon-Weaver index and a modified version of Hill's ratio (Golet et al. 2000, Tinker et al. 2008, Woo et al. 2008). Alternative indices for quantifying individual specialisation are based on diet overlap measures between the individual and population (Bolnick et al. 2002).

2.4. Diet (trophic position/carbon source) using stable isotopes

Stable isotope analysis of carbon ($^{13}C/^{12}C$, $\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$, $\delta^{15}N$) are used increasingly to test for consistency in trophic level and foraging habitat over multiple time scales. In marine ecosystems, the ratios of stable carbon and nitrogen isotopes in consumer tissues reflect those of their prey during tissue formation in a predictable manner (Phillips et al. 2009a). Carbon stable isotope ratios mainly reflect the foraging habitat or carbon source of the consumer, whereas nitrogen stable isotope ratios indicate trophic position (Bearhop et al. 2000, Cherel et al. 2006, Ceia et al. 2012). Since different tissues turn over at different rates, each integrates diet information over various temporal scales (Bearhop et al. 2006, Ceia and Ramos 2015). For instance, plasma retains information from a few days prior to sample collection, and red blood cells from the previous 3 to 4 weeks, whereas feathers and fur represent diet during moult, since keratin is metabolically inert after synthesis (Bearhop et al. 2006, Ceia et al. 2012, Barquete et al. 2013). Pinniped vibrissae (in otarids), chelonian shells and mammalian teeth sampled sequentially can be used to represent several years (Hobson and Sease 1998, Cherel et al. 2009, Vander Zanden et al. 2010). Consequently, the similarity between stable isotope ratios measured in different tissues with different turnover rates or during different periods can be used as a proxy for individual diet and habitat specialisations (Wakefield et al. 2015).

$\delta^{13}C$ or $\delta^{15}N$ are often analysed separately; however, because $\delta^{13}C$ has a trophic component, the studentized residuals of the relationship between $\delta^{13}C$ and $\delta^{15}N$ can be included in models testing for short- and long-term consistency to control for the variability in $\delta^{13}C$ that could be due to $\delta^{15}N$ (Votier et al. 2010, Ceia et al. 2012). Alternatively, a multivariate model which allows direct modelling of the covariance/correlation between these traits can be used to control for the variability in $\delta^{13}C$ due to that in $\delta^{15}N$; however, this approach, to our knowledge, has not been used in the marine predator literature to date.

The most common approach, applicable to different types of data (stable isotope ratios, trip metrics, habitat use; see below), includes the use of repeatability analysis (i.e. intraclass

correlation coefficient, ICC), where the level of individual specialisation in a population can be estimated as the proportion of the total variance accounted for by differences among individuals, according to the following formula:

$$R = \frac{\sigma_\alpha^2}{\sigma_\alpha^2 + \sigma_\varepsilon^2}$$

with σ_α^2 being the between-individual variance and σ_ε^2 the within-individual variance. The way to estimate the variance components will depend on the distribution of the data (Nakagawa and Schielzeth 2010). For Gaussian data, such as ratios of carbon and nitrogen, repeatabilities can be calculated either with the F table of an ANOVA with individual identities as fixed factors (e.g. Hamer et al. 2001, Gray et al. 2005, Patrick et al. 2014, Patrick and Weimerskirch 2014, Muller et al. 2014, Oppel et al. 2015) or with linear mixed-effects models with individual identities treated as a random effect (e.g. Dias et al. 2011, McFarlane Tranquilla et al. 2014, Grist et al. 2014, Wakefield et al. 2015). Note that the framework proposed by Bolnick et al. (2002), examining the within-individual component and between-individual component of a niche, is essentially the same as the residual variance (within-individual variance) and between-individual variance when using mixed-effects models. Indeed the ratio WIC/TNW is very similar to the equation for repeatability except that the numerator represents the within- rather than between-individual variation. Linear mixed-effect models have the advantage of directly estimating the variance necessary for the calculation of repeatability; the quantities σ_α^2 and σ_ε^2 can be extracted from the output of a mixed model. For non-Gaussian data (e.g. binary, proportion and count data), generalized mixed-effects models (GLMM) with the appropriate link function are required (eg. Potier et al. 2015, García-Tarrasón et al. 2015). The advantage of using mixed-effect models to calculate repeatability is that additional covariates can be included as fixed effects to account for known sources of variation. However, controlling for fixed effects will affect variance component (and hence repeatability) estimates (Wilson 2008; adjusted repeatabilities, Nakagawa & Schielzeth 2010). The inclusion of predictors associated with individual observations (season, year, etc.) will tend to increase the repeatability, while predictors associated with the individual level component (sex, age, etc.) will tend to decrease repeatability (Wilson 2008, Nakagawa and Schielzeth 2010). ANOVA tables use the ratio of the sums of squares to estimate repeatabilities, but do not allow the inclusion of any additional fixed effects (Lessells and Boag 1987). The statistical significance of the repeatability can be tested with a randomisation test: measurements (e.g. isotope ratios) are reshuffled many times between individuals and repeatability is calculated for each randomisation. The corresponding

p-value is the proportion of randomisations that produce a repeatability index greater or equal to the observed repeatability. This can be implemented in the R package 'rptR' (Nakagawa and Schielzeth 2010). The importance of modelling differences in within-individual variation (e.g. using (double) hierarchical generalised linear models, or (D)HGLMs) as presented in Cleasby et al. 2015) has been recognized in a variety of fields and, recently, by ecologists, but is not discussed in detail in this review because, as far as we are aware, it has featured only in few studies of marine ecology (but see Cleasby et al. 2015 for a review of indices).

In theory, when data are normally distributed and the design of the study is balanced (equal number of measurements for each individual), an even simpler approach is to test for a correlation (Spearman's or Pearson's correlation) between pairs of measurements taken at different points in time for each individual (correlation-based repeatability, Nakagawa & Schielzeth 2010). If there are more than two measurements per individual, correlations can be calculated between each pair of measurements, and averaged for each individual. The main issue with correlations is that they ignore other factors, and so this might lead to within individual consistency being high because the measurements were taken under the same conditions, rather than because the individual is consistent (Dingemanse et al. 2012).

A general question when calculating repeatability (or any other index of individual specialisation) is about sample sizes. (Wolak et al. 2012) calculated confidence intervals for a number of repeatability estimates presented in the literature and found that for most of these studies the precision was actually rather low because of inappropriate sample sizes. They provide guidelines for estimating how many individuals and how many measurements per individuals are necessary to get a certain level of precision. In general, the higher the value of the repeatability index, the less measurements and individuals are needed to get a good precision. Wolak et al. (2012) also emphasize the idea that the same precision can be achieved with different combinations of number of individuals / number of measurements. In the particular case of stable isotopes, for which there are in most cases only two measurements per individual, this means that the number of individuals needed will be rather high. However, the formula Wolak et al. (2012) provide for this estimation only applies in the case of repeatabilities calculated using the variance components of a one-way ANOVA table, hence for Gaussian data. In the case of more complex model structures and/or non-Gaussian data, no such formula exists. However, power analyses can still be carried out at the level of each variance component in a mixed models framework (potentially with both random intercepts and random slopes), using the R package 'pamm' (Martin et al. 2011).

2.5. Biologging studies

A variety of devices have been used to examine animal movements, including Platform Terminal Transmitter (PTT), Global Position System (GPS), and geolocator or Global Location Sensing (GLS) loggers. These devices have different performances, and the general trade-off is between temporal resolution, deployment duration, device mass and cost (Wakefield et al. 2009). PTTs can provide multiple locations per day with accuracy typically of <15 km (Phillips et al. 2008, Burger and Shaffer 2008, Costa et al. 2010). Due to their high cost, these devices have, to an extent, been replaced in the last decade by GPS loggers. The latter have a much better spatial accuracy (within 10 m) and temporal resolution (up to 1 Hz) (Guilford et al. 2008, Phillips et al. 2008, Kotzerka et al. 2010). In diving predators that only surface for short periods, very rapid (<100 ms) acquisition Fastloc GPS is required, and is slightly less accurate than conventional GPS (50 % of locations within 36 m; Dujon et al. 2014). Because of the very high temporal resolution, fine-scale behavioural information can be inferred from movement (Guilford et al. 2008, Freeman et al. 2010). The use of miniaturised GPS loggers, however, is still limited by the short lifespan (weeks) of devices without solar panels. The use of GLS loggers avoids some of these problems as they have low power requirements, and are small enough to be attached long-term to a ring on the tarsus or a flipper tag (Wilson et al. 2002, Phillips et al. 2004a, Shaffer et al. 2005). This technology is unsuitable for fine-scale spatial analysis, but is ideal for monitoring large-scale movements during the non-breeding season or over extended periods. Amongst the disadvantages, GLS loggers will provide only two locations per day with an average accuracy of 186 ± 114 km, and latitude is difficult to estimate from light for 3 to 4 weeks around the equinoxes (Phillips et al. 2004a, Shaffer et al. 2005). Other devices can be deployed that collect immersion, acceleration, temperature, images, acoustic or other data allowing more detailed investigations into at-sea activity (Phalan et al. 2007, Mackley et al. 2010, 2011, Gutowsky et al. 2014).

Biologging studies can be used to assess the potential specialisation or flexibility of individuals from within a population because individuals can be tracked across multiple trips or over the course of a year or longer (Pinaud and Weimerskirch 2005, Soanes et al. 2013, Muller et al. 2014). As such, the data can be used to examine repeatability in foraging destinations (i.e. site fidelity), migration schedules (timing and duration of events), fidelity to wintering areas and routes, and consistency in habitat use or preference (Croxall et al. 2005, Phillips et al. 2005, 2006, Thiebot et al. 2011, Guilford et al. 2011, Yamamoto et al. 2014).

2.5.1. Analyses of trip summary statistics

Spatial information collected by tracking devices will typically be in two dimensions (latitude and longitude). Therefore, in order to apply the methods listed above (correlations and repeatability analysis), spatial data are typically reduced via summary statistics to a single dimension, or are analysed separately (Phillips et al. 2005, Dias et al. 2013, Yamamoto et al. 2014, Ceia et al. 2014a, Potier et al. 2015). The most common summary data derived from each trip that have been used in this way include the total duration, total distance travelled (summed great circle distances between fixes), maximum range (great circle distance to the furthest location), and bearing at departure or to the furthest point (Hamer et al. 2001, 2007, Soanes et al. 2013, Patrick et al. 2014, Ceia et al. 2014a, Baylis et al. 2014, Oppel et al. 2015, Potier et al. 2015). For the non-breeding season, the analyses are often of migration schedules (timing and duration of events, (Croxall et al. 2005, Phillips et al. 2005, Dias et al. 2011, Yamamoto et al. 2014), or the total distance travelled during the migration (Muller et al. 2014). Other one dimensional data used in studies of individual specialisation include dive characteristics and activity metrics (Laidre et al. 2002, Staniland et al. 2004, Cook et al. 2005, Ratcliffe et al. 2013, Patrick et al. 2014, Potier et al. 2015, Wakefield et al. 2015).

Correlation tests can be performed to compare the above measures collected at different points in time (e.g. Phillips et al. 2005, Pettex et al. 2012, Soanes et al. 2013, Yamamoto et al. 2014). However, these tests do not allow individual specialisation *per se* to be quantified. The alternative is to carry out repeatability analyses, as presented in the previous section, e.g. of proportions of V-shaped dives (Patrick et al. 2014, Wakefield et al. 2015), wintering destinations (Perez et al. 2014) or number of dives per foraging trip (Potier et al. 2015).

2.5.2. Spatial analyses: distance between centroids of distributions or migratory routes

It is possible to study individual specialisation in space, and not only in trip characteristics, based on distances between the centroid of the locations at two different times for the same individuals tracked during the breeding season (Navarro & González-Solís 2009, Ceia et al. 2014), or between centroids in different winters (Dias et al. 2011, Yamamoto et al. 2014, Fifield et al. 2014, McFarlane Tranquilla et al. 2014). Distances can also be calculated between pairs of migratory routes (e.g. for the same individual during consecutive years), either between positions at certain landmarks (Yamamoto et al. 2014), or as the mean distance between each position on one route and the nearest position on the other (Guilford et al. 2011, Dias et al.

2013). The smaller that distance, the more consistent the individual. To compare the within- and between-individual distances (i.e. evaluate the statistical significance of individual consistency), one approach is to use distances calculated for pairs of centroids or routes as the response variable in a (G)LMM with individual (same vs. different) as a random effect, and check for the significance of the random effect (Dias et al. 2013). The second, and more widely used approach, is to compare the calculated within-individual distances with a null distribution of distances generated by reshuffling either locations or migratory tracks between individuals (Navarro and Gonzalez-Solis 2009, Dias et al. 2011, Fifield et al. 2014, McFarlane Tranquilla et al. 2014). This method based on distances does not take into account the spread of the locations around the centroids: hence, although useful to detect a shift in the general distribution, it would not detect a change only in range size. It also has the disadvantage of only allowing individual specialisation to be detected, but not quantified.

2.5.3. Spatial analyses: overlap between distributions

Specialisation can also be estimated as the overlap between distributions of the same individual over time. One approach is to overlay the locations (dives, landings or feeding events etc.) on a grid, and count the number of shared grid cells between different trips made by the same individual (Hedd et al. 2001, Baylis et al. 2014, Sommerfeld et al. 2015, Orben et al. 2015). These values are usually compared with null models based on randomization of individual identities. Problems include the sensitivities to grid cell size and to the resolution of the tracking data. Indeed, if the data are too coarse, there is a risk that genuine differences between individuals will be missed. Ideally, data should be analysed on a scale that is as fine as possible, although not smaller than the accuracy of the tracking device, but if the grid cells are too small, potentially no two points from the same bird will ever fall in the same cell even if these points are relatively close.

Probabilistic measures offer an alternative approach; a utilisation distribution (UD) is generated from tracking data, and the polygons representing core and general use areas (typically 50 % and 90/95 %, respectively) are then compared in an analysis of overlap to determine the probability of individuals being located repeatedly in the same area. This method has been used to compare foraging areas in consecutive trips during the breeding season (Phillips et al. 2006, Pettex et al. 2012, Soanes et al. 2013), and areas used from one year to the next (McFarlane Tranquilla et al. 2014, Muller et al. 2014). The problem is that it does not exploit the information

on the complete UDs (cf. Ceia et al. 2014a, Fifield et al. 2014, Wakefield et al. 2015, Ceia et al. 2015). In contrast, the indices described by (Fieberg and Kochanny 2005) provide more elegant means to represent the overlap between pairs of UDs, mainly based on the product of two UDs. They suggested the use of Bhattacharyya's Affinity (BA) when the aim is to quantify the degree of similarity among UD estimates (see Wakefield et al. 2015), and the utilization distribution overlap (UDOI) when a measure of space-use sharing is desired. Isopleths can, of course, still be informative when using these indices. The observed distribution of the indices can be compared to randomized distributions. In general for methods using UDs, care needs to be taken in the definition of the smoothing factor (*h* value) required for kernel analysis, since it can influence the resulting UD. A constant value of *h* for all individuals should be preferred (Fifield et al. 2014); otherwise, variation in behaviour can be indistinguishable from that due to the choice of smoothing parameter.

2.5.4. Environmental (habitat) analyses

Tracking data provide information not only on the geographical space, but also on how individuals use their environment (habitat). Indeed, remotely-sensed environmental data can be extracted for each animal location and, as with other types of movement information, traditionally each environmental dimension is analysed separately, typically calculating the overlap (Bhattacharyya's Affinity) between the usage distributions represented by pairs of trips for each individual (Wakefield et al. 2015). Alternatively, it is possible to include all variables in the same model, using random slope models (allowing for the response to environmental conditions to vary between individuals). This has been used to investigate how environmental conditions influence the track characteristics, e.g. speed or straightness of the path of different individuals (Patrick et al. 2014). The same approach using random slopes can also be used in a resource selection function framework in which habitat selection is estimated by contrasting environmental conditions at "used" locations (i.e. the recorded locations) and "available" locations (randomly simulated locations in the accessible area around the recorded locations), in general using a GLM with a logistic link. This can be extended to GLMMs, using random slopes (individuals as a random effect) to detect differences between individuals in selection for each variable.

2.6. Controlling for pseudo-repeatability

Some effects can create bias in the estimation or interpretation of levels of individual variation, which can inflate repeatability estimates, leading to pseudo-repeatability (Dingemanse and Dochtermann 2013). This inflation occurs when predictor variables (i.e. fixed effects) that influence within-individual variation vary between individuals because of a sampling or measurement error; or when biologically relevant parameters (i.e. fixed effects) that explain between-individual differences are not taken into account in models (Dingemanse and Dochtermann 2013, Westneat et al. 2015). Other explanations proposed for heterogeneity in residual within-individual variance are the "Organismal error" (when the variance in phenotype is due to errors made by individuals when assessing their environment, e.g. individuals misidentify the cue to the environment and produce a response which would be better suited to another environment) and the "Random residual within-individual variance" (when variation is due to a random process; e.g. stochastic variation in density and location of prey), which are discussed in detail in Westneat et al. (2015).

Several issues related to temporal scale exist. Indeed, consistency detected at different time scales has different ecological interpretations (see Réale and Dingemanse 2001 for a related discussion on the study of animal personality). If individuals are consistent over a short but not over a long timescale, the "specialisation" detected is likely to be due to variation in the state of the individuals (e.g. hunger level or reproductive state), or other short-term uncontrolled effects (e.g. immediate environmental conditions). If individuals are consistent over a long time scale, the cause is likely to be due to genetic, parental, individual quality, or possibly, permanent environmental, effects. If specialisation increases over long time scales, the causes are likely to be related with some learning process (over the lifespan of an individual) or selective disappearance (over several generations, i.e. if specialists are fitter, generalists will selectively disappear from the population). This emphasizes the importance of carrying out studies that, ideally, cover multiple time intervals (Kernaléguen et al. 2015).

Conversely, incorrect combination of time periods can lead to erroneous interpretations. Indeed, if individuals specialise on different resources or environments over different seasons, studying specialisation over the whole year, for example, might prevent the detection of individual specialisation (the latter can be controlled by including the correct fixed effects). In the case of seabirds, although several studies have revealed that dietary and behavioural specialisations are widespread, it is unclear for how long these specialisations are maintained (Masello et al. 2013, Patrick et al. 2014); but see Wakefield et al. 2015). It is likely, however, that repeatability in

foraging behaviour declines at longer temporal scales because of temporal changes in the availability and predictability of resources (Woo et al. 2008, Bell et al. 2009, Ceia et al. 2014a). Weimerskirch (2007) also suggested that site fidelity not only depends on the timescale, but also on the habitat visited. Almost all published studies to date were limited to data from relatively few individuals tracked or observed over short periods of time (Žydelis et al. 2011). Novak & Tinker (2015) also raise this point for time-aggregated observations related to diet, noting that increasing sampling time increases knowledge of an individual's diet but comes with the risk that the ability to detect meaningful temporal patterns in prey selection is reduced.

The timing of the study can also bias the results for reasons that are not necessarily linked to individual preferences. For example, if individuals are tracked only during consecutive trips or for a few consecutive years, when conditions may be more similar than after longer intervals, the lack of within-individual flexibility in behaviour may reflect either that there was no environmental change influencing prey availability, or site fidelity (Chilvers 2008, Pettex et al. 2012, Carneiro et al. 2016). However, if tracked for multiple years with contrasting environmental conditions and prey availability, the repeated use of an area would indicate site fidelity. The latter, however, can also reflect behavioural plasticity, which is hard to tease apart.

Timing, as well as spatial accessibility, are also important when studying between-individual differences. If all individuals in the study do not have access to the same environment or prey (either because the conditions change, or because individuals live in distant areas with different characteristics), then the population might exhibit apparent specialisation, even though individuals are not specialised. Thus, to be sure that it is indeed specialisation that is observed, studies should minimise the risk of differences in habitat or resource availability between individuals, which in practice is a major challenge. Note that this can to some extent be resolved by combining trophic markers such as stable isotope ratios with tracking in multiple years (Baylis et al. 2014).

Finally, populations can exhibit different foraging behaviours depending on the season (e.g. for seabirds, even within the breeding season, energy requirements and the constraint of the colony usually differ between pre-laying, incubation, brood-guard and later chick-rearing). It is important to take these changes into account otherwise apparent individual differences might arise as an artefact of mismatches in the temporal scale of the measurements.

2.6.1. Effects specific to stable isotope data

Studies using stable isotopes as a measure of individual specialisation/consistency in resource use should ideally use methods that allow the partitioning of isotope variation between different factors, and individual effects, such as calculating the adjusted repeatability from mixed-effects models. It is also possible to control for some of this variation during sample collection and preparation. Factors that should be taken into account when estimating short- and long-term spatial consistency or dietary specialisation (δ^{13}C and δ^{15}N values) relate to: (1) the comparison of tissue types with different enrichment factors for carbon and nitrogen isotopes (Cherel and Hobson 2007, Quillfeldt et al. 2008), (2) the use of tissues with different turnover rates (e.g. plasma and red blood cells), but with some overlap in terms of diet integration period (Votier et al. 2010, Ceia et al. 2015), (3) the differences in baseline isotope ratios in foraging areas used by individuals (in the marine environment, different oceanic processes and sources of organic matter can result in spatial changes in baseline stable isotope ratios; Moreno et al. 2011), and (4) the variation in baseline isotope ratios between different periods and years (Araújo et al. 2011, Wakefield et al. 2015). In addition, intrinsic factors, which are linked to physiological and life history traits (sex, breeding stage, experience, reproductive status etc.) can also be taken into account, although this will tend to decrease repeatability estimates (see Wilson 2008 for a discussion).

Tissue type

Keratinous tissues such as feathers, fur, vibrissae and chelonian shells are enriched in ^{13}C and ^{15}N when compared with blood, even when synthesized over the same time periods, due to different protein sources, use of endogenous reserves during feather synthesis, or when plasma contains ^{15}N-depleted uric acid (Hobson et al. 1996, Cherel et al. 2005, Cherel & Hobson 2007, Quillfeldt et al. 2008). Lipid concentrations can also lead to particularly depleted δ^{13}C values (Bearhop et al. 2000, Votier et al. 2010). Lipid extraction from fatty tissues is therefore recommended prior to δ^{13}C analysis (Cherel & Hobson 2007, Wakefield et al. 2015). However, extraction techniques can affect δ^{15}N in an unpredictable manner (Cherel et al. 2005, Bond and Jones 2009, Wakefield et al. 2015). Ideally, two samples, one to measure δ^{13}C (delipidated) and one to measure δ^{15}N (non-delipidated), should be analysed (Paiva et al. 2010, Wakefield et al. 2015). The low lipid level of keratinous tissues, blood cells and of whole blood does not affect their δ^{13}C, and so lipid extraction is not required (Cherel et al. 2005, Bond and Jones 2009,

Matich et al. 2011, Ceia et al. 2012, 2015). High and varying concentrations of lipid in blood plasma, however, can result in depleted $\delta^{13}C$ values (Votier et al. 2010, Ceia et al. 2012, 2015). Lipid extraction can often be impracticable because of the small quantities of blood plasma (Votier et al. 2010, Wakefield et al. 2015, García-Tarrasón et al. 2015). In order to account for the remaining potential differences in enrichment factors, correction factors can be used (Cherel et al. 2005, Quillfeldt et al. 2008, Votier et al. 2010, García-Tarrasón et al. 2015) or tissue type included as a fixed effect in adjusted repeatability analysis (Wakefield et al. 2015).

Overlap in diet integration periods

Several studies have modelled short-term consistency in isotope ratios by comparing values between plasma and red blood cells collected in a single event (e.g. Ceia et al. 2012, 2014a, Wakefield et al. 2015, Ceia et al. 2015). Although each tissue has a different turnover rate, the integration of prey isotopes into body tissues is a continuous process, and the analysis of short-term consistency using the same blood sample inevitably leads to some overlap in the periods which the samples represent (Votier et al. 2010, Ceia et al. 2015). To overcome this issue, when combined with tracking analysis, some studies have collected blood in two sampling events associated with the capture (deployment) and recapture (retrieval) of tracking devices, using the red blood cell fraction from initial capture and the plasma fraction from the recapture for subsequent analysis (Votier et al. 2010, Ceia et al. 2015), or only the plasma collected during both events (García-Tarrasón et al. 2015).

Spatial and temporal variation in isotopic baselines

Marine isoscapes can change depending on nutrient source, primary productivity, depth, latitude and oceanic frontal region, which can confound direct comparisons of trophic levels between animals from different regions (Stowasser et al. 2012, Moreno et al. 2015). Information on isotopic ratios of potential prey from different foraging areas (which can be determined from tracking devices) are essential for distinguishing the relative importance of prey vs. habitat specialisation (Moreno et al. 2016). Otherwise, it is not possible to tell if a change in isotopic value from t_1 to t_2 (or tissue type x and y) represents a wider diet or spatial niche, or the same diet consumed in areas or periods with different isotope baselines (Ceia et al. 2014a, Moreno et al. 2015). The latter applies in particular to species that forage across environmental boundaries and change their foraging areas on a seasonal basis (Stowasser et al. 2012). However, because

most marine organisms are associated with specific water masses, even when apparent differences in trophic position are most likely related to the use of areas with different baselines, dietary differences may still be informative about the use of particular prey (Jaeger et al. 2014). To date, there has been only one study including estimates of baselines as fixed effects in adjusted repeatability analysis of $\delta^{13}C$ and $\delta^{15}N$ in the blood of northern gannets *Morus bassanus* from the Bass Rock, within and across years (Wakefield et al. 2015).

2.6.2. Effects specific to tracking data

Studies of behavioural consistency and individual specialisation based on tracking data should, where possible, apply a variety of complementary approaches. It is straightforward to include fixed factors in analyses of summary statistics, but more difficult to control for these effects in spatial analysis. For the latter, the analyses have to be carried out separately for each level of those factors (e.g. males and females treated separately), but this implies the need of bigger sample sizes. In addition to sex and age effects, life-history stage and breeding status (failed or successful) can potentially influence foraging strategies and therefore should also be considered when testing for individual specialisation. Breeding status, for example, may not only affect timing of events (e.g. Croxall et al. 2005, Phillips et al. 2005, Dias et al. 2011, Bogdanova et al. 2011, Yamamoto et al. 2014), but also the use of migratory destinations and routes. When this information is not known, such effects can be reduced by restricting comparisons to particular time windows, for example to minimize the risk that apparent differences between individuals might relate to differences in migration schedules that ultimately took similar routes (Guilford et al. 2011). Behaviour may also differ between different types or phases of foraging trips (outward and return journeys, and hunting and searching for food), or migration (outward and return migration, and residence at the main staging and wintering areas). For birds during chick-rearing, different types of trips can be performed by adults while provisioning their chicks; short trips to maximize delivery rate per unit of time and long trips that enable adults to restore their own reserves (Weimerskirch et al. 1994, Weimerkirch 1998); but see Phillips et al. 2009). All these potential differences need to be taken into consideration when analysing individual specialisation, as the constraint to return sooner to the colony can prevent individuals from visiting areas that would otherwise be optimal.

2.7. Conclusion

Individual specialisation can be calculated by using repeated measurements for each individual, then calculating the within- and between-individual variation. Although there are several alternatives (see Table 2.1), the most common and flexible approach is to calculate repeatability, using the variances extracted from GLMMs with individual as a random effect (either random intercepts or random slopes). To obtain estimates of *individual* specialisation, care needs to be taken to exclude effects that can lead to pseudo-repeatability. In addition, analysing a variety of data types simultaneously can provide better insights. Analysis and interpretation can be improved if a representative number of individuals are studied that have access to the same habitat and resources (preferably over the same periods), and over short and long timescales. Statistical analyses of individual differences should be rigorous and follow advice mentioned in this review. Studies that conformed to these recommendations have found convincing evidence of behavioural consistency and individual specialisation in marine predators, albeit typically over relatively short timescales, as well as in a wide range of other taxa (e.g. Woo et al. 2008, Patrick et al. 2014, Ceia et al. 2014a, Wakefield et al. 2015). In contrast, the ecological implications of consistent differences in resource or habitat selection at the individual or population level remain unclear (Ceia & Ramos 2015). However, such differences are likely to affect the conclusions of population dynamics models (as does individual consumer behaviour or trait variation; Okuyama 2007, Schreiber et al. 2011). Indeed, individual specialisation can affect interactions between individuals (e.g. by reducing intraspecific competition, Bolnick et al. 2011). Such differences may also reduce the predictive power of existing ecological models, for example species distributions models that are used increasingly to predict the response of a species to climate change or following an introduction (Pearman et al. 2008), wherein projections are made from average values for the population. Indeed, if individuals differ in their environmental tolerance (or preferences), species-environment relationships inferred from only a sample of individuals might not be representative of the ability of the species to cope with change.

Although in this review we have presented the most common methods used by the marine ecology research community to study individual specialisation and behavioural consistency, it is important to note that there have been a number of interesting methodological developments in the animal personality field which build on repeatability analysis to ask targeted research questions, especially related to within- vs. between-individual variation, and partitioning of

variance components (van de Pol and Wright 2009, Dingemanse and Dochtermann 2013). Several of these methods have the potential to be applied to marine predators.

2.8. Acknowledgements

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3. A new method to quantify individual specialization using tracking data: a case study on two species of albatrosses

3.1. Abstract

Many predictive models of the spatial and temporal distribution of species (e.g. in response to climate change or species introductions) assume that species have one environmental niche that applies to all individuals. However, there is growing evidence that individuals within a species can have environmental preferences that are narrower than the species niche. Such individual specialization has mainly been studied in terms of dietary niches, but a recent increase in the availability of tracking data opens the possibility of extending these analyses to specialisation in terms of environmental preferences. Yet, no study to date on individual specialisation considered the environmental niche in its multidimensionality. Here I propose a new method for quantifying individual specialisation in multiple dimensions simultaneously by comparing hypervolumes in n-dimensional environmental niche space of an individual versus an overall population, as well as a test of significance by comparing observed values against a null model. The same method can be applied to a 2-dimensional geographic space to test for site fidelity. I applied this method to test for individual environmental specialisation (across three dimensions: sea surface temperature, eddy kinetic energy, depth) and for site fidelity among 12 individual black-browed albatrosses (*Thalassarche melanophris*) and 10 grey-headed albatrosses (*Thalassarche chrysostoma*), tagged in the same colony in South Georgia and tracked during their breeding season. I found evidence for site fidelity in both species and of environmental individual specialisation among grey-headed albatrosses, but no evidence for individual specialisation among black-browed albatrosses.

3.2. Introduction

The spatial distribution of a species is influenced by a range of environmental conditions, underpinning the ecological concept of a species niche, classically referred to as an *n*-dimensional hypervolume in environmental space (Hutchinson, 1957). There are two broad types of conditions (Peterson et al. 2011): those linked dynamically to the population under study (e.g. resources that are consumed, which can be studied directly or indirectly), and those that are not consumed and for which no competition occurs (scenopoetic variables; Hutchinson 1978). Understanding the relationships between species and their environment allows the development of predictive models of species distributions in space or time (Elith and Leathwick 2009, Wakefield et al. 2011, Scales et al. 2016), including in response to climate change or to species introductions (Elith et al. 2010, Gallardo and Aldridge 2015, Vicente et al. 2016). These models assume a common niche for the whole species or population, but in reality, this niche is the combination of individual preferences or tolerances. Whilst in principle all individuals can have the same broad niche as the species (i.e. generalist individuals), there is often some specialisation at the individual level (Bolnick et al. 2003). Accordingly, there is a growing awareness of the importance of considering intra-specific variation in niches, and in the development of analytical methods that test for this robustly (Bolnick et al. 2011, Carneiro et al. 2017, Phillips et al. 2017).

Quantifying individual specialisation requires observing repeated choices made by each individual. For prey selection, such repeated choices are easy to observe, as each meal is potentially an independent replicate. Numerous studies have shown evidence of individual diet specialisation in a wide range of taxa (Bolnick et al. 2003, Araújo et al. 2011, and Phillips et al. 2017 for reviews). However, extending the study of individual specialisation to foraging site and environmental preferences is more complicated: if individuals are sedentary, it is impossible to know whether they could tolerate broader conditions than those at the site where they are found, as only one choice of environment is observed. Species that are very mobile, on the other hand, provide good study models for quantifying environmental specialisation, as animals undertaking long-distance movements can potentially sample a wide range of environmental conditions and make a series of choices (i.e. where to travel next). Such data are increasingly available because of the recent improvements in tracking devices, including their improved accuracy and miniaturisation (Wakefield et al. 2009, Ropert-Coudert et al. 2009, Bridge et al. 2011). Previous studies have focused on individual differences in behaviour (e.g.

timing of migration: Phillips et al. 2005, McFarlane Tranquilla et al. 2014; diving strategies: Ropert-Coudert et al. 2003; Patrick et al. 2014), geographical specialisation or site fidelity (e.g. to migration route or wintering area: Phillips et al. 2005, Dias et al. 2011; or foraging site during the breeding season: Patrick and Weimerskirch 2014, Wakefield et al. 2015). Fewer studies have investigated environmental specialisation (Phillips et al. 2017); however, these often find some evidence of consistency in the use of certain habitat types or environmental conditions (Phillips et al. 2009a, Catry et al. 2014, Wakefield et al. 2015, Fodrie et al. 2015).

The paucity of studies on environmental specialisation is partly due to methodological limitations. Quantifying environmental specialisation requires a comparison of the environments utilised by individuals across a series of repeated choices of locations (typically breeding or foraging areas) with those utilised by the population as a whole (see Carneiro et al. 2017 for a review of existing methods). When environmental space can be classified into discrete habitat units (e.g. Catry et al. 2014, Fodrie et al. 2015), traditional methods developed for examining consistency in prey choice can be applied (see Bolnick et al. 2002). However, in many cases, no discrete environmental classification is possible without using arbitrary thresholds and loosing information, and continuous variables have to be considered. Preference distributions can be estimated for each variable (reflecting the proportion of time spent in locations characterized by each value of the variable), for each independent choice of environmental conditions (e.g. for each breeding season or for each foraging trip). The similarity in preference between each independent choice of conditions (e.g. using Bhattacharyya's affinity) reflects the degree of individual consistency (Wakefield et al. 2015). However, because of the need to calculate Gaussian kernels in several dimensions simultaneously, this approach currently only allows one or two variables to be analysed at a time. This is a key limitation, because the niche is usually better described by more dimensions, especially if there are interactions. There is therefore a pressing need for a method that quantifies individual specialisation in more dimensions simultaneously.

Here I develop and test a new method for quantifying individual specialisation in multiple environmental dimensions, applying it to two species of seabirds as case studies. Seabirds are particularly suited for the study of individual environmental specialisation, as they can move long distances and the accessibility of different environmental conditions can be considered to be similar for all individuals in a given population at the same breeding stage. Seabirds can also be tracked with relative ease, particularly the larger species that can be fitted with devices with

long battery lives, and detailed information on their environment can be accessed through satellite remote-sensing (Wakefield et al. 2009). Furthermore, as most seabirds breed in dense colonies, divergent foraging strategies might be expected if these reduce intraspecific competition (Bolnick et al. 2011). Finally, as many seabirds are threatened by human activities, it is important to understand the degree of specialisation in foraging strategies within populations, which will influence the potential for adaptation to environmental change, as well as decisions relating to monitoring and conservation priorities (Phillips et al. 2017).

I focus on the grey-headed albatrosses (*Thalassarche chrysostoma*) and the black-browed albatrosses (*Thalassarche melanophris*) as case studies. A degree of non-breeding site fidelity and individual consistency in timing of migration was found in grey-headed albatrosses (Croxall et al. 2005), and for black-browed albatrosses individual behavioural differences have been detected in various traits, including at-sea activity patterns (Mackley et al. 2010), trip duration and maximum distance from the colony during chick-rearing (Patrick and Weimerskirch 2014), and site fidelity during the non-breeding season (Phillips et al. 2005). Individual habitat specialisation has also been detected in black-browed albatrosses during the breeding season (Patrick and Weimerskirch 2014, 2017) but using habitat categories (shelf vs. shelf edge vs. oceanic waters; Patrick and Weimerskirch 2014) or only one environmental variable (bathymetry; Patrick and Weimerskirch 2017), thus ignoring the multidimensionality of the niche. In contrast, Granadeiro et al. (2014) found no evidence of individual specialisation in this species in diet or carbon source (a proxy for habitat) using stable isotope ratios. Whereas some of these studies suggest there may be a degree of individual specialisation (in behaviour, foraging locations or habitat), so far none has tested whether this translates into differences in the multi-dimensional environmental niche. The new method I present here for quantifying and testing individual environmental specialisation, the Individual Specialisation Index (ISI), accounts for multiple dimensions simultaneously. I detail the rationale for the method as well as the details of its implementation, and how it can be used in a statistical test of individual specialisation. I then apply it to extensive tracking data from the two albatross species, both to investigate individual site fidelity (in two dimensions in geographic space) and environmental specialisation (in three dimensions in environmental space).

3.3. The Individual Specialisation Index (ISI)

3.3.1. Rationale

The most common approach used to estimate individual specialisation is based on comparing the within-individual and between-individual variances (e.g. Nakagawa and Schielzeth, 2010, Bolnick et al. 2003; see Carneiro et al. 2017 for a review of methods). When interpreting the results, one should however keep in mind that although the within-individual variation is usually assumed to be directly linked to the level of individual specialisation, it can also encompass other sources of variation (measurement error, differences between biologically relevant categories (e.g. sex), random residual variation or organisms misinterpreting cues and using environments that do not correspond to their prefences, Westneat al. 2015).

The *ISI* is a generalisation of the approach used in Bolnick et al. (2003) for diet data. For a single continuous variable describing dietary items (e.g. prey size), Bolnick et al. (2003) define the total population niche width (*TNW*) as the variance in the values of this variable pooled over all consumed items. TNW can be partitioned into a between-individual component and a within-individual component (*WIC*, the average variance of resources in individual diets; Figure 1). The ratio $\frac{WIC}{TNW}$ provides information on the level of individual generalism (and 1-$\frac{WIC}{TNW}$ on individual specialisation) within the population.

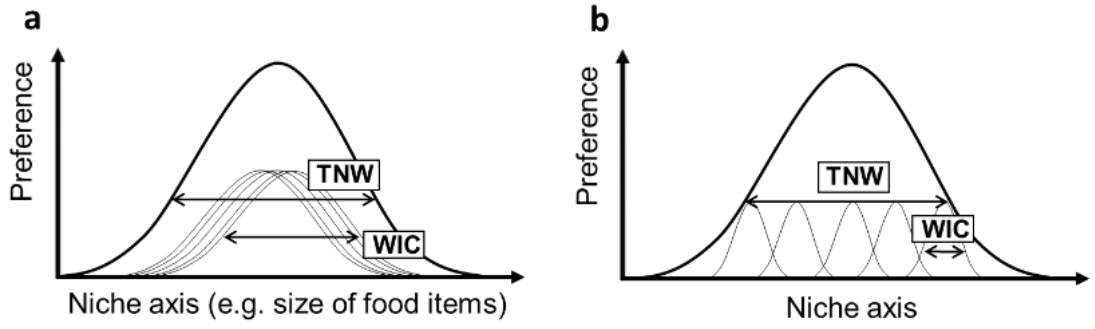

Figure 3.1: A schematic diagram of how individuals (thin lines) can subdivide the population's niche *(thick line) (adapted from Bolnick et al. 2003). TNW: total niche width, WIC: within-individual component: a) a population of generalist individuals, b) a population of specialist individuals.*

I extended this approach to the study of environmental preferences. For this I used tracking data made of multiple trips per individual. For each trip, characterised by geographic locations (X_n, Y_n), where *n* is the track length, environmental conditions are extracted at each (X_i, Y_i). Each individual is then characterised by a set of points in as many dimensions as the number of environmental variables considered. Note that the method requires covariate data for each point. The within-individual component for each individual (WIC_i) is calculated as its hypervolume, and the total population niche width as the hypervolume enclosing all the locations visited by all the individuals in the study. The Individual Specialisation Index is defined as:

$$ISI_i = 1 - \frac{WIC_i}{TNW}$$

High values of the ISI correspond to individuals that are highly specialised compared with the population they belong to; low values of the ISI correspond to generalist individuals. Note that in the original approach in Bolnick et al. (2003), there is only one average WIC value calculated for the whole population. My extension, however, calculate a value for each individual, a way to take into account the problems raised by (Cleasby et al. 2015), that there can be between-individuals differences in within-individual variation.

3.3.2. Hypervolume construction

In order to estimate niche widths, hypervolumes of use are built in niche space (environmental space) by extending a method previously developed for two-dimensional geographical space: the Local Convex Hull (LoCoH) method (Getz et al. 2007). See section 3.5.1. for a discussion of the reasons why I retained this approach compared with other methods. In particular, I selected the LoCoH method rather than traditional Gaussian kernel methods for its ability to deal with holes and sharp boundaries and for ease of implementation at the time of this project. Among the three versions of the LoCoH method, I focused on the so-called adaptive-LoCoH. For each focal point, I first find the maximum number of nearest neighbours such that the cumulative distance between the focal point and its neighbours is less than or equal to a threshold parameter *a*. Note that I take *a* to be the same for all individuals. I then build the smallest convex polyhedron containing these points (By comparing the median of ISIs over the sampled population with the median for the same number of randomised individuals, it is possible to determine whether the population is composed of generalist or specialist individuals. If the empirical value of the individual specialisation index is higher than that expected by

chance (95% CI of the null distribution),C-F); polyhedra are thus smaller where the density of points is higher. To build a polyhedron in n dimensions, a minimum of $n+1$ points is needed; points with less than n+1 neighbours satisfying the distance criterion are ignored, providing a filter for outliers. For a given individual, all valid polyhedra are then merged together to obtain the n-dimensional niche hypervolume.

However, as combining n-dimensional polyhedra is mathematically and computationally challenging, I calculate the overall volume of each individual's niche hypervolume by first intersecting all the focal individual's polyhedra with a multidimensional grid (i.e. checking which cell centroids are included in each polyhedron), and then computing the overall volume as the number of cell centroids that are included in at least one of the constituting polyhedra. The same procedure is used for estimating the population volume, calculated as the number of cell centroids that are included in at least one of all polyhedra of all individuals. To decide the appropriate grain size for the grid, the volumes of the polyhedra are calculated for decreasing grain sizes until values stabilise. I developed a simple implementation of this algorithm in R that can deal efficiently with up to four dimensions.

The construction of the polyhedra relies on the choice of parameter a: when a increases, more neighbours are included in each polyhedron, decreasing the number of holes in the overall hypervolume. However, a larger a also means a less precise volume around the points, including parts of the environmental space that are never encountered by the individual. The best value for this parameter can be chosen by visually assessing in 2D (for pairs of dimensions) the fit of the total hypervolume to the data points for different values of a (e.g. Fig A2).

3.3.3. Test of individual specialisation

The ISI provides a value of specialisation for each individual in the population. In order to test whether individuals are more specialised than expected by chance, empirical ISI values can be compared with a null distribution obtained by randomising data across individuals. The most appropriate randomisation strategy will depend on the study system (population, season, stage etc.), which can place particular constraints on individual movement and choices (e.g. seabirds are central-place foragers during the breeding season, and trip duration is restricted by the demands specific to incubation and chick-rearing duties; Phillips et al. 2017).

By comparing the median of ISIs over the sampled population with the median for the same number of randomised individuals, it is possible to determine whether the population is composed of generalist or specialist individuals. If the empirical value of the individual specialisation index is higher than that expected by chance (95% CI of the null distribution),

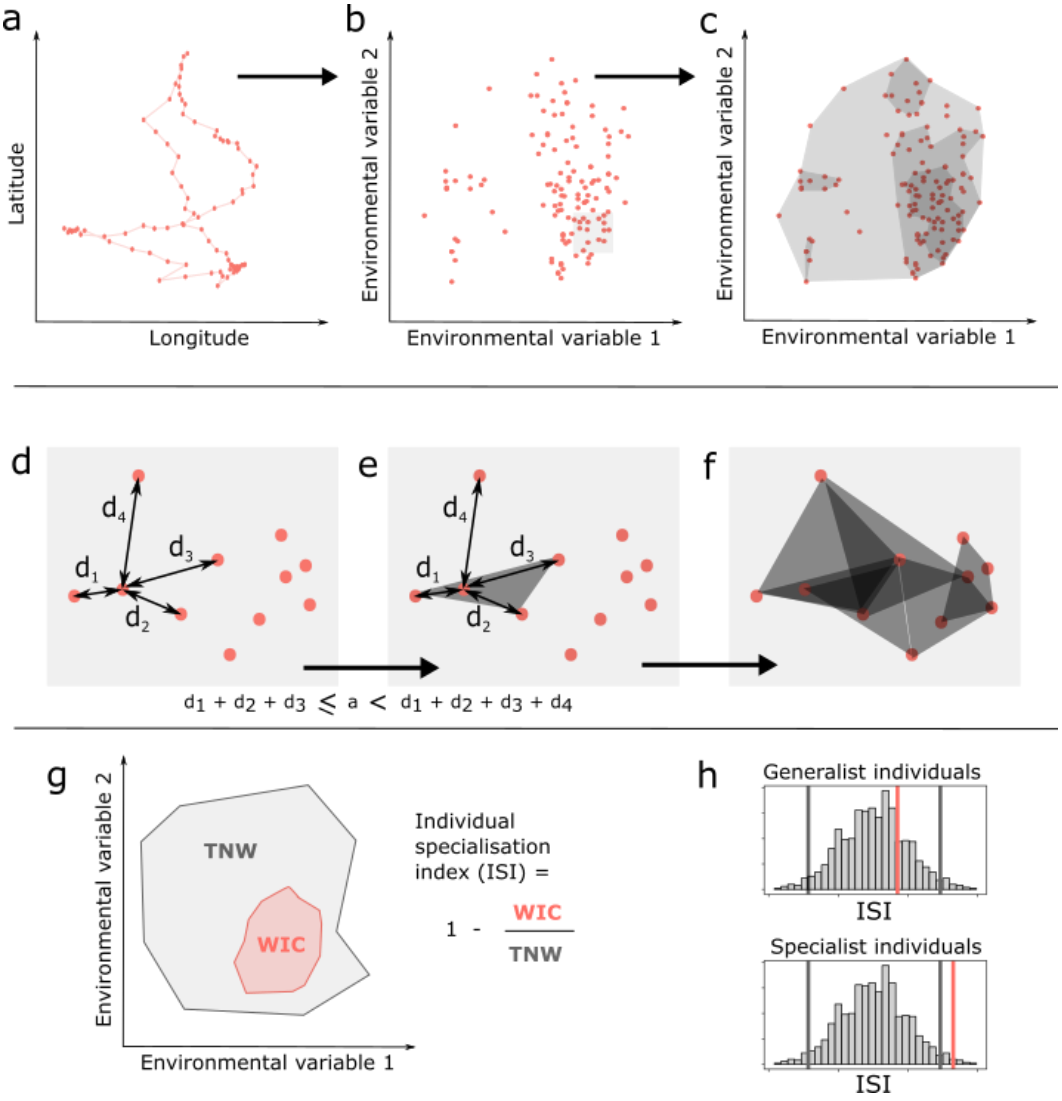

Figure 3.2: Steps for calculating the multidimensional individual specialisation index (ISI), illustrated here in two dimensions. *a): Hypothetical track in geographical space: each point corresponds to a location record. b) Position of location records in a 2D environmental space. c) Hypervolumes around the locations in environmental space. d)-e): Selection of neighbours around a focal point. Neighbours are included from the closest to the furthest, until the sum of the distances between the focal point and its neighbours reaches the value a. Creation of the hypervolume containing all these selected points. f) Repetition of the previous step for each focal point. g) Calculation of the index based on the volumes of the individual hypervolume (WIC: within-individual component) and of the population hypervolume (TNW: total niche width). h) Test of individual specialisation: null distribution of individual specialisation values, grey: 95% CI, red: median of empirical ISI values. If the empirical ISI values fall within the 95% CI of the null distribution, individuals are considered no more specialised than expected by chance. If the empirical ISI values are higher than the 0.975 quantile of the null distribution, individuals are considered more specialised than expected by chance.*

then the population can be considered made up of specialists (By comparing the median of ISIs over the sampled population with the median for the same number of randomised individuals, it is possible to determine whether the population is composed of generalist or specialist individuals. If the empirical value of the individual specialisation index is higher than that expected by chance (95% CI of the null distribution),H); otherwise, it can be considered to constitute generalists. Individual ISIs can also be compared directly to contrast degrees of specialisation between individuals.

3.4. Application to empirical data: albatross tracks

3.4.1. Tracking data

I used tracking data of grey-headed albatrosses (GHA) and black-browed albatrosses (BBA) from Bird Island, South Georgia (54°00′S; 38°03′W), collected during the post-brood chick-rearing stage of the breeding season. These data consist of locations obtained from Platform Terminal Transmitters (PTTs, see Phillips et al. 2004b for deployment details) for 124 trips of 5 male and 5 female GHA between February and March 2001, and 270 trips of 6 male and 6 female BBA between January and March 2002, which corresponds to the chick-breeding period (post-guard). See Tables A1 and A2 for summaries of the two datasets. Wet-dry (saltwater immersion) loggers were also deployed on BBA (Phalan et al. 2007), providing information on foraging activity. Locations were projected using the South Pole Lambert Azimuthal Equal Areas projection.

Locations in my datasets were at irregular time intervals (average interval ± SD of 1.3 ± 1.3h, and 1.3 ± 1.0h for GHA and BBA, respectively). To avoid the problem that the distribution of raw locations may not be representative of the actual time spent in each set of environmental conditions, locations were interpolated hourly intervals using the R package *adehabitatLT* (Calenge 2015).

3.4.2. Environmental data

I selected variables reflecting oceanographic processes that are likely to affect individual choices in terms of location: sea surface temperature (SST), eddy kinetic energy (EKE), and

depth. These variables have been shown previously to predict the distribution of albatrosses and other seabirds at the species level (see Wakefield et al. 2009 for a review, and Wakefield et al. 2011 for black-browed albatrosses in particular) and are proxies for where preys can be found. For SST, hypothesized to limit the distribution of prey species and a proxy for productivity (Wakefield et al. 2011), I used a weekly composite with a spatial resolution of 0.25°, obtained from the NOAA website (http://www.esrl.noaa.gov/). For EKE, a proxy for mesoscale activity, I used a weekly composite with a spatial resolution of 0.25°, downloaded from the AVISO website (www.aviso.oceanobs.com). For depth, used because different bathymetric regimes present different levels of productivity (Wakefield et al. 2011), I used a raster with a spatial resolution of 1' downloaded from the NOAA website (www.ngdc.noaa.gov/mgg/global/). For each bird location, I extracted the value for SST and EKE on the closest date on which remote-sensing data were available, using the *raster* package (Hijmans and van Etten 2014) in R.

I initially considered the inclusion of chlorophyll *a* concentration (Chl-a). However, maps of Chl-a concentrations contained a high proportion of missing values at high latitudes due to cloud cover (57% missing values for BBA, 40% for GHA when using a weekly composite from the NOAA website: http://coastwatch.pfel.noaa.gov/). Since my method requires an environmental estimate for each spatial position visited by the bird, Chl-a would have required excessive spatial interpolation.

3.4.3. Analyses

3.4.3.1. Selection of relevant locations

I removed transit locations based on a residence-time approach (Barraquand and Benhamou 2008), using the package *adehabitatLT* (Calenge 2015) in R.3.2.2 (R Development Core Team, 2015). This approach is based on the time spent in a circle of a certain radius around each focal point: locations around which individuals spend little time (as delineated by a chosen threshold, see details below) are interpreted as transit locations; conversely, locations around which individuals spent a lot of time are interpreted as foraging or resting locations (birds making sinuous tracks or area-restricted search. First, I selected a radius of 45km, obtained by multiplying the mean transit speed (which for BBA and GHA is 45km/h, the best glide speed; Wakefield et al. 2009) by the interval between sampling locations (1 hour) (Torres et al. 2017). Second, in order to translate the residence times into categories of behaviour, I used the

distribution of residence times (Figure A1) to select a threshold value of 25,000 seconds (between the two peaks of the bimodal distribution). All locations corresponding to a shorter residence time were classified as transit, and all locations above that threshold were classified as foraging. To avoid using locations when birds might be drifting on the water (i.e. to separate resting from foraging), I considered only locations during daylight, when albatrosses are most likely to be foraging (Phalan et al. 2007). Timings of sunset and sunrise were calculated for each location using the *StreamMetabolism* package (Sefick Jr 2016) in R. See Tables A1 and A2 for the remaining number of locations per individual. As a validation of this approach to eliminate transit locations, I used wet-dry transitions (landings and take-offs) from immersion loggers, available only for BBA. As in Phalan et al. (2007), I characterised each 10-min bout as a "wet bout" if the bird spent more than 3s on the water. Daytime locations were characterised as foraging if at least one bout in the surrounding hour (interval between two locations) was considered "wet". For each of these two approaches, I generated plots to visually inspect any differences, calculated the ISI values and tested their significance.

3.4.3.2. Individual specialisation in environmental space

I assessed the level of individual environmental specialisation by applying the ISI approach to multi-dimensional environmental space (three-dimensions: SST, depth, EKE). I log-transformed EKE values to reduce overdispersion and standardised all variables to give the same weight to all dimensions. Flat polyhedra (arising when many points have similar coordinates in at least one dimension) led to computing problems with the R package *geometry* (Habel et al. 2015). To prevent this, I added a negligible random jittering (following a uniform distribution between -5e-5 and +5e-5) to each value.

3.4.3.3. Individual foraging site fidelity

Specialisation in certain environmental conditions can be driven by several mechanisms, including specialisation in geographical space (i.e. "site fidelity"). The ISI method applied in geographical space provides information on the width of the space use of each individual relative to that of the population. I thus calculated individual foraging site fidelity in this way for BBA and GHA. Note that, as projected coordinates are in the same unit, I did not standardize them prior to analysis.

3.4.3.4. Null model

I built a null model for each species to test whether the ISI values obtained were different from the distribution expected by chance. To do so, I generated "null individuals" by randomly selecting subsets of all trips (e.g. Figure 3.5). By keeping trips as whole units, I ensured that the null model took into account the spatial and temporal autocorrelation that exists within trips. I simulated 100 sets of as many null individuals as those in our dataset (12 for BBA and 10 for GHA) and calculated the ISI values for each of these sets, thus generating a null distribution of expected ISI values. I then compared the empirical ISI values with these distributions as a test of the extent to which they were significantly more specialised than expected by chance. For each species, and for each analysis (in geographic and in environmental space), I made two types of tests: at the individual and at the population level. At the individual level, each empirical value was compared with the whole distribution of null ISI values. At the population level, the median of the empirical values for individuals was compared with the distribution of median values calculated for each null population (one median per set of 12 or 10 individuals). In both cases, significance of the one-way test was assessed by calculating the proportion of null values higher than the empirical one.

3.4.4. Results

3.4.4.1. Data selection

Comparison between the two methods for classifying activity (residence time vs. immersion data) indicated that the areas inferred to be foraging locations were similar (Figure 3.3). Moreover, the method used to identify foraging locations did not influence the conclusions of the ISI analysis (Figure 3.4 and Figure 3.6: in neither case was individual environmental specialisation detected for the BBA population). I was therefore confident that using presumed foraging locations selected using residence time was effective, and subsequent results were from these locations only. The final dataset in my ISI analyses included 1507 and 4243 locations, corresponding to 19 % and 27% of the interpolated locations for GHA and BBA respectively (Figure 3.3)

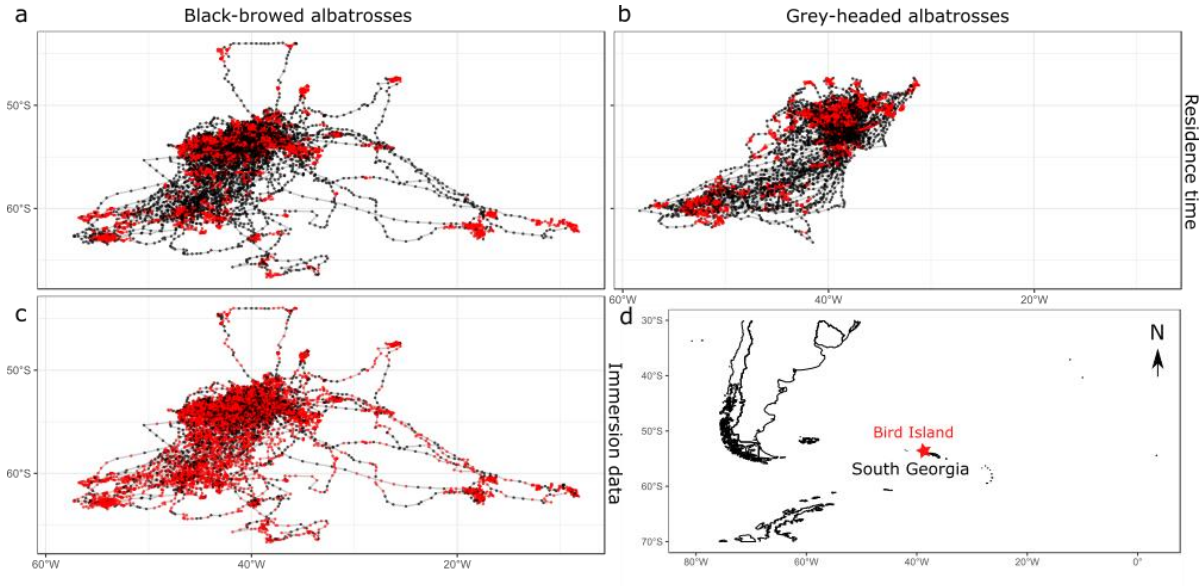

Figure 3.3: Locations where birds were considered to be foraging (red points) vs. in transit or resting (black points)*: a) results for black-browed albatrosses (BBA) based on residence time, b) results for grey-headed albatrosses (GHA) based on residence time, c) results for BBA based on immersion data. Immersion data were not available for GHA. d) Location of the colony (Bird Island, South Georgia).*

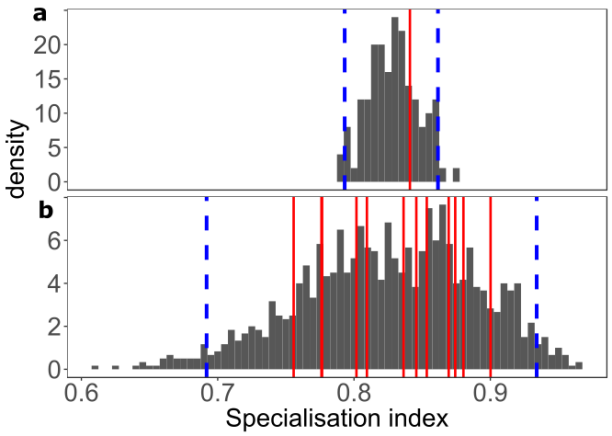

Figure 3.4: ISI values for BBA when locations were selected using immersion data: comparison between the null model *(histogram; vertical blue dotted lines: 95% CI)* ***and the empirical values*** *(vertical red lines), in geographical space (site fidelity): a) median population values; b) individual values. Results are consistent with Figure 3.6 when locations were instead selected using Residence Time.*

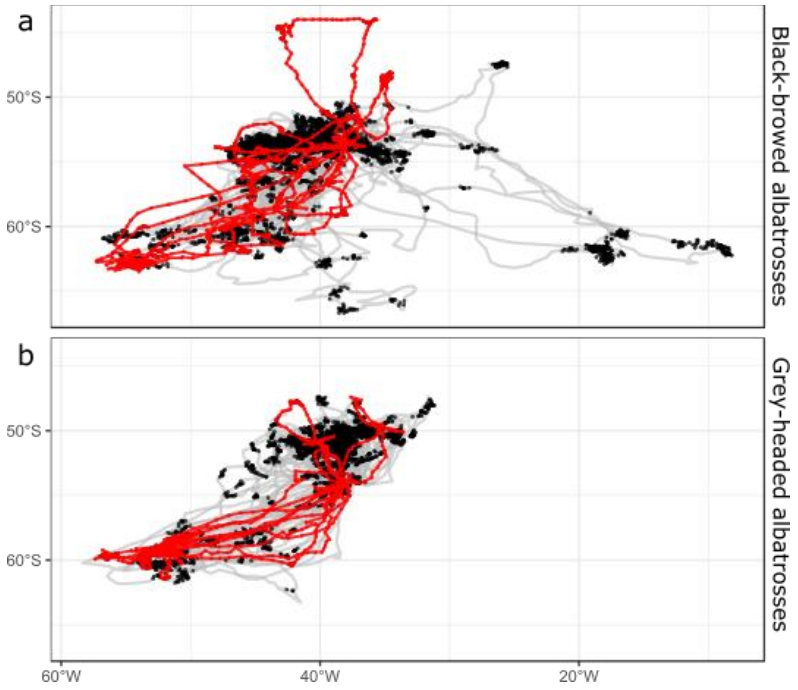

Figure 3.5: Examples of repeated trips by one individual contrasted with those of other individuals in the dataset*: a) BBA; b) GHA. Grey: foraging trips of all sampled individuals. Red: foraging trips of one individual selected at random. Black dots: selected foraging locations used in the analysis.*

3.4.4.2. Application of the ISI method: choice of parameters

In geographical space, when *a* was ≤ 200km, some locations were not included in the hypervolumes, and the latter were too fragmented for further analysis (Figure A2). At the other extreme, when *a* was ≥ 600km, the hypervolumes included too many areas that did not contain data points (Figure A2). I thus retained an intermediate adaptive-LoCoH parameter *a* = 400 km. In environmental space, I excluded values a < 2 because the hypervolumes were too fragmented and a > 4 because the hypervolumes covered too many areas with no data points (Figure A3 to Figure A5) and retained *a* = 3 for all subsequent analyses. Comparison between the results obtained for three different values within the realistic range of *a* in environmental space (*a* = 2, 3 and 4: Figure A3 to Figure A5) shows that the significance of the test was not affected by the value of *a*.

Selected grid cell sizes were 25km and 0.125 in geographical and environmental space, respectively, which were a compromise between accuracy (Figure A6 and Figure A7) and

computational time. Note that when variables are standardised (in environmental space), parameters (*a* and grid cell size) are unitless.

3.4.5. Tests of individual specialisation

3.4.5.1. Individual site fidelity

Both BBA and GHA showed significant individual site fidelity; empirical ISI values in geographical space were higher than expected by chance (Figure 3.6). The effect was the strongest for BBA.

3.4.5.2. Individual environmental specialisation

There was no evidence of significant individual specialisation in three-dimensional environmental space (EKE, SST and depth) for BBA (Figure 3.7). In contrast, individual GHA were significantly more specialised in three-dimensional environmental space than expected by chance (Figure 3.7B).

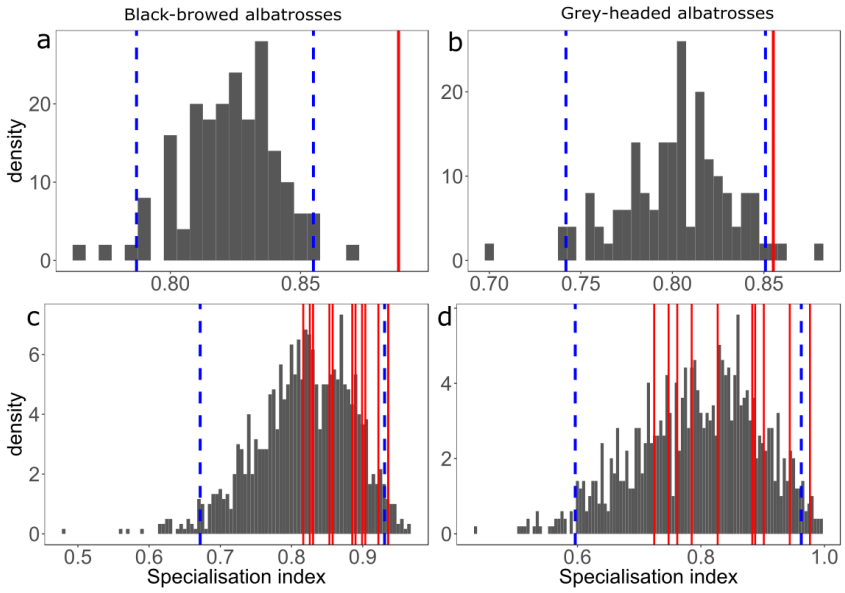

Figure 3.6: ISI values: comparison between the null model *(histogram; vertical blue dotted lines: 95% CI)* ***and the empirical values*** *(vertical red lines), in geographical space (site fidelity). a) Median population values for black-browed albatrosses (BBA); b) median population values for grey –headed albatrosses (GHA); c) individual values for BBA; d) individual values for GHA. All birds were tracked during chick-rearing at South Georgia.*

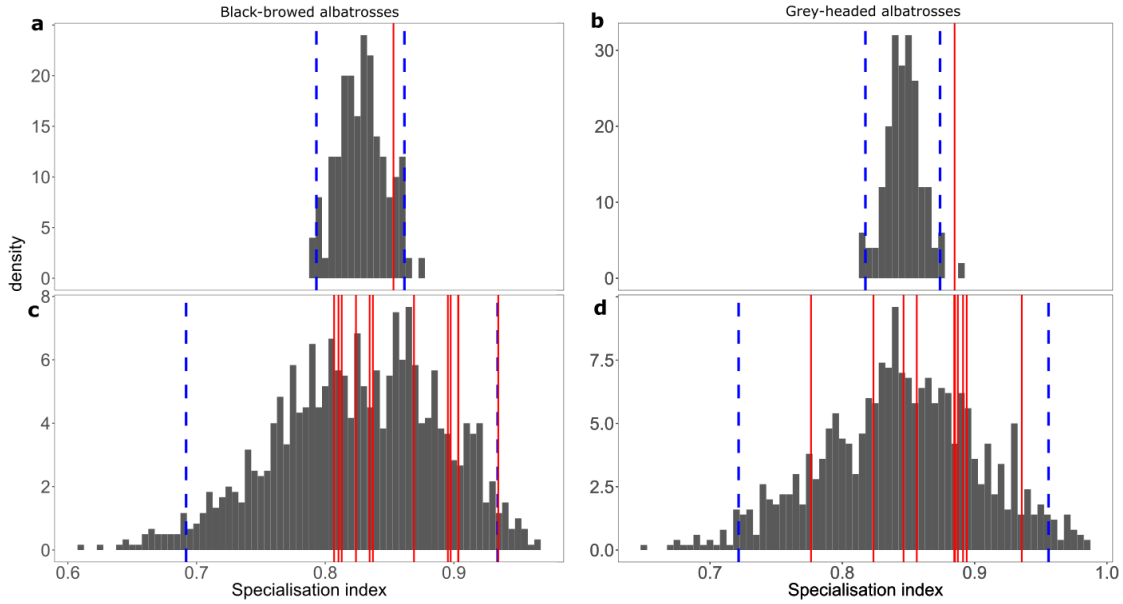

Figure 3.7: ISI values: comparison between the null model *(histogram; vertical blue dotted lines: 95% CI)* ***and the empirical values*** *(vertical red lines), in three-dimensional environmental space (environmental specialisation). a) Median population values for black-browed albatrosses (BBA); b) median population values for grey-headed albatrosses (GHA); c) individual values for BBA; d) individual values for GHA.*

3.5. Discussion

3.5.1. Measuring individual specialisation in multiple dimensions

In this chapter, I present a method for quantifying individual site fidelity and consistency in habitat use from repeated observations of the same individuals, based on the hypervolumes of usage in a multidimensional space. Application of this approach in geographical space tests for site fidelity, and in environmental space for individual habitat specialisation. The basis of any study of individual differences is to contrast within-individual and between-individual variance components. Most studies of individual differences have used the repeatability framework (Nakagawa and Schielzeth 2010), where the between- and within-individual variance components are estimated via (Generalised) Linear (Mixed) Models. Repeatability is traditionally used in behavioural studies, for example in analyses of trip summary statistics (Patrick et al. 2014, Potier et al. 2015), such as path straightness, number of dives, bearing or maximum distance from the colony, but can also be used for studying habitat selection. In that case, environmental variables are included as fixed effects, and individual identities as random

effects. This provides a separate measure of repeatability for each variable, but not a summarised output for each individual. More importantly, although interactions between variables can be included, the linear mixed-model approach does not directly take into account the multidimensionality of the niche. Here, I chose instead to extend the approach presented in Bolnick et al. (2003), which is a form of repeatability analysis but the within- and between-individual components are not calculated by estimating the parameters of linear models. My novel formulation provides a single and readily interpretable index of specialisation for each individual, allowing for a robust statistical test of individual specialisation, in situations when the environment is better characterized in multiple dimensions. The approach also presents various advantages over other methods for comparing distributions or habitat preferences. For example, unlike measures of distance between centroids of distributions (both in geographical - e.g. Navarro and González-Solis 2009, Ceia et al. 2014b, and in environmental space - e.g. Patrick and Weimerskirch 2017), my approach takes into account the width of the niche. This is important as specialisation requires not only the mean of the distributions to differ between individuals, but also the spread of individual preferences to be narrow compared with the spread of preferences of the population as a whole.

To extend Bolnick's approach to environmental conditions (habitat use), I had to estimate the within- and between-individual variances (and hence the total variance, to which they sum) in multiple dimensions. For that purpose, I built hypervolumes around points in a multidimensional space by generalizing the LoCoH method for estimating utilisation distributions in two dimensions (Getz et al. 2007). An alternative would have been to analyse parametric kernels, which are also used to estimate utilisation distributions in two dimensions. The R package *hypervolume* (Blonder et al. 2014) provides an approximation of these hypervolumes and their characteristics (e.g. volume). However, such parametric kernel methods often fail to capture features such as holes (but see Blonder 2016) or other sharp boundaries (Getz et al. 2007). Although more computationally intensive, the method proposed in this chapter has the advantage of being able to deal with sharp boundaries, and of not expanding outside the environmental conditions of the most extreme locations, whatever the choice of the shape parameter.

Irrespective of the kernel method that is used, decisions need to be made concerning the parameters influencing the hypervolume construction. For Gaussian kernels, the choice of bandwidth has a major influence on the size of the hypervolume: if too small, the hypervolume

typically has holes in the environmental spaces in regions between observations, although these may actually be part of the niche; if too large, the hypervolume is likely to expand far beyond the environmental space that is actually visited by the individual. Using the LoCoH approach, the shape parameter *a* also needs to be selected, mainly based on visual evaluation. However, it is possible to exclude some values of *a* visually, either because too many points are excluded from the hypervolume, which contains too many holes (e.g. *a* = 200km in Figure A2), or because the hypervolume includes too many areas which do not contain points (e.g. *a* = 800km in Figure A2). Regardless, the test is robust to the choice of this parameter for a range of realistic *a* parameters (Figure A8). The grain size of the grid used to estimate the volume of the hypervolumes also needs to be appropriate, but as demonstrated in this paper, it can be chosen empirically by increasing granularity until the volume estimates stabilise.

3.5.2. Considerations in the use of movement data for understanding the contribution of individuals to the niche of a species

Estimating site fidelity or individual environmental specialisation requires data from a series of independent choices made by each individual. In particular, individual environmental specialisation can be studied by comparing environmental conditions (often derived from satellite remote-sensing data) in repeated choices of geographical locations to which animals are tracked on consecutive trips. In this study, I used PTT data for two species of central-place foragers which made multiple trips from their colony during chick-rearing. Given that within each trajectory there is a degree of spatial autocorrelation (because once a decision is made to travel in a particular direction, the options are then restricted to the environment and areas available in the surroundings), I considered the foraging trip as my unit of study. My method thus requires having a sufficient number of tracks per individuals. I have assumed that each foraging trip constitutes an independent choice of foraging areas, but there are limitations to this assumption First, if the study is based only on portions of tracks (in this application: foraging trips) that are consecutive, there is a risk that individuals return to a location because they successful obtained prey there on the previous trip (win-stay lose-shift strategy), and not because of long-term site fidelity or environmental specialisation (but see Wakefield et al. 2015 for a discussion on how these can be disentangled). It is thus important to use a time series of tracks that is sufficiently long that the decisions can be considered sufficiently independent, with the limitation that periods in which behaviour may change markedly are analysed separately (e.g. habitat selection often differs between the breeding and non-breeding seasons,

because the central-place spatial constraint is removed and thus the availability of environmental conditions may differ markedly; Phillips et al. 2017). Second, even if portions of tracks can be considered independent from one another, they do not necessarily constitute distinct choices. For example seabirds, and in particular the two species of albatrosses studied here, can be strongly constrained by wind (Weimerskirch et al. 2000), which influences their spatial distributions (Phillips et al. 2004b, Weimerskirch et al. 2012). Failing to account for such wind effects might be misleading: for instance, two birds leaving the colony on the same day might make similar trips not because they have similar environmental preference but because they experience the same wind conditions. Also, an individual might not return to the same place from one trip to the next, not because the place is unsuitable, but because the wind conditions would make this inefficient. However, in my study, I removed transit locations to focus on foraging areas: hence, although wind can influence the general direction (and thus the identification of site fidelity), it should be less of an issue for environmental specialisation, because of the redundancy of environmental conditions in geographical space (i.e. the same environment can be found in different places, and albatrosses cover great distances whilst foraging).

3.5.3. Characterising the niche: strength of environmental drivers and accessibility

The relevance of any analysis of individual specialisation in environmental space relies on the strength of the relationship between the species under study and its environment. This relationship is both related to how strongly the environment affects the distribution of the species (i.e. the strength of the biological constraints), and the extent to which the environmental variables that matter have been incorporated in the study (which depends on available data, as well as on the analyst's capacity to identify the important habitat variables at the appropriate scale). Thus, failure to detect individual specialisation can either mean that it does not exist, or that the environment has been incorrectly characterised. An inaccurate characterisation of the environment can arise from neglecting some important environmental variables were neglected, or from measuring them at the wrong scale. For example, here I used weekly instead of more fine-grained daily data (see Scales et al. 2017 for a discussion of scale issues). I did this because daily data were too incomplete (mainly because of cloud cover preventing efficient remote sensing at these latitudes), but this could potentially impair my ability to detect relevant individual preferences (in particular if prey patches are less persistent than the temporal scale of the environmental variables I considered).

Additionally, and contrary to model-based approaches (e.g. resource selection functions), my method requires all individuals to have access to the same environmental conditions, so that comparing choices of foraging locations between individuals is equivalent to comparing environmental preferences. My method is thus particularly suited to study individual specialisation in central-place foragers (e.g. in this study, all individuals are constrained by the need to return to the same colony, so they all begin and end their foraging trips at the same location), even though central-place foragers are also more constrained in their choices of foraging locations (reducing the scope for specialising). Furthermore, even though the notion of accessibility also depends on the scale of study (once the first decision about direction is made, the available foraging areas are no longer the same for all individuals), the redundancy of environmental conditions in space would allow specialised individuals to access patches of their preferred habitat even in a different foraging area.

3.5.4. Ecological significance

In my study, both BBA and GHA were found to be site-faithful, although the effect was the strongest for BBA. By comparison, only the GHA population appeared to be composed of individuals specialised in environmental space (habitat). I can be confident that the environment that is relevant for albatrosses was adequately described because my analysis included variables that were found previously to influence habitat use at the species level in both BBA and GHA (Wakefield et al. 2011, Scales et al. 2016). Hence, my results indicate that individual BBA do not differ in their habitat use with respect to the variables measured. This may be for two reasons: either individual birds use the same resources, or they specialise on different resources but these are not strongly linked to the environment. Indeed, even if resource specialisation exists, the scope for environmental specialisation to emerge depends on the level of predictability of the resource according to environmental cues (e.g. for site fidelity: Baylis et al. 2012, Wakefield et al. 2015). In particular, the higher the trophic level of a species, the more indirect the relationship between the environment and the distribution of its prey (Grémillet et al. 2008). The results found here for BBA diverge from those of Patrick and Weimerskirch (2017) for BBA from Kerguelen, which showed a stronger environmental specialisation (for water depth) than site fidelity, but are similar to those for northern gannets *Morus bassanus*, for which fidelity to the site is much stronger than that to the environment (Wakefield et al. 2015).

A possible explanation for the contrast between the results by Patrick and Weimerskirch (2017), who found evidence of individual specialisation in BBA from Kerguelen, and my study in South

Georgia, where I did not, may relate to the predictability of environmental conditions and resources in the surrounding waters. Prey availability in neritic habitats is considered to be more predictable than in the open ocean, and probably explains the high incidence of individual specialisation in near-shore species such as shags and cormorants (Phillips et al. 2017). BBA at Kerguelen forage far closer to the colony than adults from South Georgia, and spend a much higher proportion of their time in shelf waters (Figure 3.2; cf. Weimerskirch et al. 1997; Pinaud and Weimerskirch 2002). Moreover, SST within the foraging range at Kerguelen was found to be more stable between-years than that at South Georgia in a previous study comparing demography in the two populations (Nevoux et al. 2010). Other inequalities between the two sites could also influence the degree of specialisation, such as the greater diversity of available foraging habitats in the southwest Atlantic compared with the Indian Ocean (Phillips et al. 2009b). Alternatively, the differing results might relate to the relative constraint on foraging trip duration in each breeding stage. Indeed, my data were obtained during post-guard chick-rearing, whereas the previous study was during brood-guard (when the chick is attended by one parent, greatly limiting the time that the partner can spend at sea). However, in theory, greater constraints during brood-guard might reduce opportunities for specialising on different habitats. Indeed, adults in post-guard can target a wider range of habitats over a much larger area, which should reduce competition and hence the benefit of specialisation. Finally, the different results may be due to the different methodologies; the study at Kerguelen compared centroids of foraging areas (both in terms of geographic distance and differences in depth), which does not take into account the spread of the distribution (i.e. the variability in conditions used during each foraging phase). It also placed much less emphasis on the within-individual variance component, whereas my more robust comparison of niche width is likely to constitute a more conservative test of individual specialisation.

Relative predictability of environmental conditions and resources may also explain the stronger evidence for specialisation in foraging location in GHA than BBA at South Georgia. During chick-rearing, GHA foraged both north of South Georgia, at the Antarctic Polar Front (APF), and over deep Antarctic waters, whereas BBA foraged mostly in open waters, or in shelf and shelf-slope waters locally or on the South Scotia Ridge, and very rarely at the APF (Figure 3.3). This corresponds to the differences in diet between species in the study years: for GHA birds, diet in 2001 was dominated by cephalopods (~75% vs. only ~9% Antarctic krill *Euphausia superba*; British Antarctic Survey, unpublished data), whereas that for BBA diet was composed of krill (~52%) and fish (~30%). The bulk of the squid are probably captured at the APF, where

they are predictable to some extent as this is a favoured foraging area for GHA throughout the year (Xavier et al. 2003b, 2003a, Clay et al. 2016). Although Antarctic krill are found in shelf, shelf-slope and deep waters around and to the south of South Georgia, there is huge spatial variation in their relative abundance, and concentrations are highly unpredictable in the open ocean (Silk et al. 2016).

3.5.5. Conservation implications

Tracking data are used increasingly to help identify key foraging sites that could be included in a network of marine protected areas (Lascelles et al. 2016, Tancell et al. 2016), or for understanding potential spatial overlap with fisheries (Phillips et al. 2005, Pichegru et al. 2009, Žydelis et al. 2011). However, resources for research are limited, and my results have implications for how these might be best-targeted. If all individual animals behave in a similar way (i.e. are generalists), then effort should be focused on a thorough understanding of what each individual does, i.e., it is better to track fewer individuals for a long period of time. On the contrary, if most animals in the population are specialists, efforts should be dedicated to tracking as many individuals as possible, even if for shorter periods. This holds not only with regard to specialisation in foraging areas (i.e. site fidelity), but also environmental preferences. Indeed, understanding the environment selected by individuals provides information on the processes and mechanisms driving geographic distributions, allows the integration of dynamic variables, and is thus useful to predicting distributions based on future environmental conditions (e.g. climate change, or in relation to seasonal and annual variation). Besides, as there is some degree of redundancy of environmental conditions in geographical space, fewer individuals are needed to characterise all the environments than the locations (areas) used by the population. Nevertheless, although my results indicate that the balance should be towards intensive rather than extensive sampling of individuals, this needs to be nuanced by the possibility that individuals with a different strategy might exist but have been missed by my sampling.

3.5.6. Potential for further applications of the method

The framework presented here offers the advantage over previous methods in that it provides a value for the level of individual specialisation of each individual within the population, thus allowing ranking and tests for the short- or long-term consequences of such specialisation. This contrasts with previous studies, which usually compare groups of specialists and generalists (Phillips et al. 2017). Hence my approach can be adopted in short-term studies investigating the

relationship between degree of individual specialisation and foraging efficiency, and long-term studies which link it to breeding success and carry-over effects (e.g. in Patrick and Weimerskirch 2017).

My method can also be used to test hypothesis regarding the causes of individual specialisation. In this chapter, I only used data from adult breeders, so my conclusions only hold for this category of individuals. However, with the appropriate dataset juveniles and adults from the same colony could be compared, providing insights into the learning processes driving foraging site selection. I would expect younger individuals to be less specialised than adults, and the onset of greater specialisation to indicate when learning occurs. Differences in movement capacities between juveniles and adults have been found in several species, including wandering albatrosses (*Diomedea exulans*) (Riotte-Lambert and Weimerskirch 2013, de Grissac et al. 2016) and Cory's shearwaters *Calonectris diomodea* (Péron and Grémillet 2013). Increases in site fidelity with age have also been recorded (in Weddell seals *Leptonychotes weddellii*, Cameron et al. 2007, in sanderlings *Calidris alba*, Lourenço et al. 2016, and in northen gannets *Morus bassanus* Votier et al. 2017), but to my knowledge, there has been no study comparing the degree of environmental specialisation between adults and juveniles. Patrick and Weimerskirch (2017) found no effect of age on the degree of site fidelity or individual specialisation, but they only studied adults which will have largely passed through the learning period.

Finally, this framework can also be used to investigate other ecological questions, such as the influence of trophic level on the degree of individual specialisation in different species or the influence of the environment on the emergence of individual specialisation (e.g. depending on the level of resources, and so on the level of intra-specific competition, the advantages of specialism will change). Providing the habitat can be properly described and enough (independent) data are available for each individual, it would be informative to apply this method to a wide range of taxa, to understand more aspects of the individual component of niches.

3.6. Acknowledgements

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4. Intraspecific migratory patterns: a test for leapfrog and chain migration using ringing data

4.1. Abstract

Within migratory species, not all individuals follow the same strategy: some migrate more than others, sometimes to the point that some individuals even remain resident all year. In his 2008 influential book, Ian Newton categorised within-species migratory strategies: individuals can follow a chain migratory pattern (i.e. all individuals migrating roughly the same distance regardless of where they come from) or they can do leapfrog migration (i.e. individuals at the more extreme parts of the range (often in terms of latitude) migrating over individuals in the more central parts of the range). Alternatively, species can also fall in none of these two categories, with individuals randomly missing when going from their breeding to their non-breeding range (and conversely). However, although some examples of these textbook patterns had been reported in the literature, a large-scale quantitative test of this classification has was yet to be done. Here, I develop a test for the existence of leapfrog or chain strategies vs. random mixing, and apply it to a ringing/recovery dataset of 9 North American migratory species. I find that in my sample, the textbook patterns are not as widespread as I could expect: most species redistribute randomly from one season to the next.

4.2. Introduction

A wide diversity of animal species perform migrations, in which "individuals make regular return movements, at about the same times each year, often to specific destinations" (Newton 2008). Such movements have been particularly studied in birds and are of primary conservation importance. Indeed, by living in and crossing multiple habitats, migratory species are especially vulnerable to global change and habitat destruction (Newton 2008). Additionally, such movements can potentially have consequences for the spread of infectious diseases (either increasing the risk of infection by connecting disjoint areas, or reducing it by allowing individuals to escape contaminated areas, Altizer et al. 2011), emphasizing the relevance of having a good knowledge of species' migratory patterns.

Migratory strategies are not uniform within species: ringing data (e.g. Jenkins et al. 2002, Catry et al. 2005, Marques et al. 2009) counts of birds at different times of the year (e.g. Meller et al. 2016), and, more recently, genetic (e.g. Liu et al. 2012), individual tracking (e.g. Dias et al. 2013, Ramos et al. 2015) and isotopic studies (e.g. Ceia et al. 2014b) have found substantial variation at the individual level within a single species. For example, in some species, only part of the population is migratory ('partial migration', e.g. Nilsson et al. 2006, Jahn et al. 2010, Pérez et al. 2014) and previous studies found that this can have various fitness consequences for the individuals favouring one strategy over the other (e.g. resident American dippers have a higher annual productivity, whereas migrants, despite having a higher survival, have an overall lower lifetime fitness, Gillis et al. 2008).

Among migratory individuals, there can be substantial variation in the distances travelled (e.g. Prescott 1991, Jenkins et al. 2002, Mathot et al. 2007), sometimes associated to morphometric differences (e.g. wing chord allometry varying with migratory distance in Western sandpipers *Calidris mauri*, O'Hara et al. 2006). When mapped across the full geographic distribution of a species, these individual differences in migratory behaviour may nonetheless reflect a coherent migration strategy at the species level. Newton (2008) proposed a classification into two main types of migration, according to patterns of latitudinal replacement of populations: chain and leapfrog. Chain migration happens when subpopulations shift their range in the same direction during migration (e.g. in terrestrial environments, Chiffchaffs *Phylloscopus collybita*, European Goldfinches *Carduelis carduelis*, Linnets Carduelis cannabina, White Wagtails *Motacilla alba*, Newton 2008; or, in marine environments, Northern gannets, *Morus bassanus*; Fort et al. 2012). In this case, there may be a part of the range where the species is resident (i.e. found year-round), but individuals are not, with winter migrants replacing summer migrants and vice

versa. On the other hand, in leapfrog migration, individuals in the most extreme parts of the range migrate over individuals in the more central parts of the range (e.g. Bell et al. 1997, Kelly et al. 2002, Panuccio et al. 2013, Ramos et al. 2015). In this case, there may be a central region, where the breeding and non-breeding ranges of the species overlap, where the individuals are indeed residents, over which migrant individuals leapfrog. Newton proposed a third category of migration, 'telescopic', when one of the ranges is much narrower than the other, such that all individuals from the wider range migrate to similar latitudes in the following season. This, however, is more about the relative sizes (i.e. latitude span) of non-breeding and breeding ranges than about the pattern of rearrangement of individuals across seasons (indeed, individuals in telescopic migration can, for example, move in a leapfrog fashion if they tend to reverse their relative latitudes across seasons). Here I focus on the distinction between chain and leapfrog migrations.

Although multiple examples of chain and leapfrog migration have been reported in the literature, studies tend to cover only part of species' ranges (e.g. for leapfrog migration: the western portion of the breeding range of Wilson's warblers, Kelly et al. 2002, or the European part of the range for marsh harriers, Panuccio et al. 2013) or focus on only on a few individuals (e.g. with geolocators for Bulwer's petrels, Ramos et al. 2015). Most analyses tend to focus on the specifics of a particular species or population, so we do not know how widespread these textbook scenarios are. Furthermore, determining whether a species follows chain or leapfrog migration is typically qualitative, rather than through a formal test against the alternative possibility that individuals may be moving randomly instead (for an exception, see Boland 1990, who however focused on the sub-population rather the individual scale).

Here, I propose two statistical tests for distinguishing whether a given species follows chain vs. leapfrog migration against the null expectation that individuals redistribute randomly, applicable to individual-level movement data across different seasons. I then apply these tests to 9 North-American bird species, taking advantage of a continent-wide dataset of ring recoveries covering both the breeding and non-breeding range of these species.

4.3. Methods

4.3.1. Two statistical tests for categorizing species migratory strategies

In each of these tests, I start by formalising the expected patterns if individuals within a species follow chain or leapfrog migration, as well as under the null expectation that they redistribute

randomly across seasons. I then propose a method for describing the empirical pattern and for comparing it with the expected patterns, testing the significance of the deviation from the null expectation.

I focus here on within-species latitudinal patterns of migration, because migrations for the birds under study are expected to take place mainly on a North-South axis. However, this test could be applied to a different axis for other organisms, such as an altitudinal axis.

4.3.1.1. Test 1: Expected patterns for the relationship between latitude and migratory distance

I assume that, for each individual, two latitudes are known: one in the breeding and one in its non-breeding season. I define the migratory distance as the difference between the breeding and the non-breeding latitudes.

If one plots the latitude of each individual in each of the two seasons against the migratory distance, different patterns are expected according to the type of migration (Figure 4.1). A V-shape (each leg of the V corresponding to one season) is obtained if individuals re-distribute randomly, because of a geometric effect whereby the longest distances are only possible by individuals migrating from the most extreme latitudes in each season (and, conversely, the shortest distances by individuals migrating from the least extreme latitudes) (Figure 4.1A). The exact shape of the V depends on the relative distance between the breeding and non-breeding ranges: a narrow V if they extensively overlap; and a shallow V if they are very distant. If individuals follow a perfect chain strategy, they would all migrate the same distance irrespective of latitude. As a result, there should be no relationship between latitude and distance, at any season (Figure 4.1B). In a less perfect scenario, any V-shaped pattern significantly shallower than the one expected under a random distribution points to a rearrangement of individuals that tends towards chain migration. In contrast, a V pattern that is significantly narrower than expected from a random rearrangement indicates a leapfrog migration (Figure 4.1C).

Given a scatterplot of the empirical data showing latitude for the two seasons against migratory distance per individual, it is possible to derive the line that best fits the data for each season through a principal component analysis (PCA) for the corresponding cloud of points. To prevent a few outliers from driving the axes decomposition, I recommend removing points with too high a leverage. This can be done by first deriving a PCA with all points and calculating the leverage for each point. Outliers can be defined as points for which the leverage is higher than

the third quartile of leverages plus three times the interquartile range (the standard definition of outliers for boxplots). The PCA is then repeated with the new dataset, excluding these outliers.

To make the loadings interpretable, I recommend not scaling the variables prior to the PCA. The main axis of the PCA represents the fitted line. The slope of this line can be inferred from the corresponding loadings, by dividing the loading for the original vertical axis (i.e. migratory distance) by the loading for the original horizontal axis (i.e. latitude). For ease of interpretation, the slopes can be converted into angles (in degrees) using the following formula: $\arctan(\frac{loading\ for\ migratory\ distance}{loading\ for\ latitude}) * \frac{180}{\pi}$. Table 4.1 presents a summary of the possible cases.

To test whether the calculated slopes diverge from what would be expected under a 'random mix' scenario, I propose the following null model: all non-breeding locations are randomly matched with breeding locations (without replacement) and the corresponding distance calculated for each pair. The above-described PCA can then be applied to the cloud of points in each season, and the slope of the first axis recorded. By repeating this procedure a large number of times, it is possible to obtain a null distribution of slopes per season, against which the empirical values can be compared to assess if for any given species the data support chain (shallower slopes than expected), leapfrog (steeper slopes) or a random mix migratory strategy (within the range of the null distribution).

4.3.1.2. Test 2: Expected patterns for resident individuals under different strategies

In species for which there is an overlap between the breeding and the non-breeding ranges, there may be individuals that are resident (i.e., that remain in the same location across seasons). Different migratory strategies should produce different patterns regarding these resident individuals. Under perfect chain migration, there should be no migratory individuals (Figure 4.1A), the resident part of the range being obtained as breeding migrants are replaced by non-breeding migrants and vice-versa. Under perfect leapfrog migration, all individuals in the resident part of the range should be resident themselves, migrants leapfrogging over them. In the random mix scenario, resident individuals can be distributed anywhere within the resident range, mixed with migratory individuals.

Given the same scatterplot as in the previous test, which describes the distribution of observed latitudes in each season against migratory distance per individual, the resident range corresponds to the range of latitudes (within the x-axis) within which it is possible to find both breeding and non-breeding individuals. Within this range, resident individuals can be defined as those with zero migratory distance (or close to zero, smaller than a pre-defined interval). It

is then possible to calculate, for any empirical dataset, the fraction of resident individuals within the resident range.

As in the previous test, it is possible to derive a null model for the expectation under the random mix scenario, by randomly matching breeding and non-breeding locations without replacement, and calculating the migratory distance within each pair, from where the fraction of resident individuals can then be derived. By repeating this many times, one can obtain a null distribution of the fraction of residents, against which the empirical values can be contrasted. A lower than expected fraction points towards chain migration, whereas a higher than expected value points towards leapfrog migration.

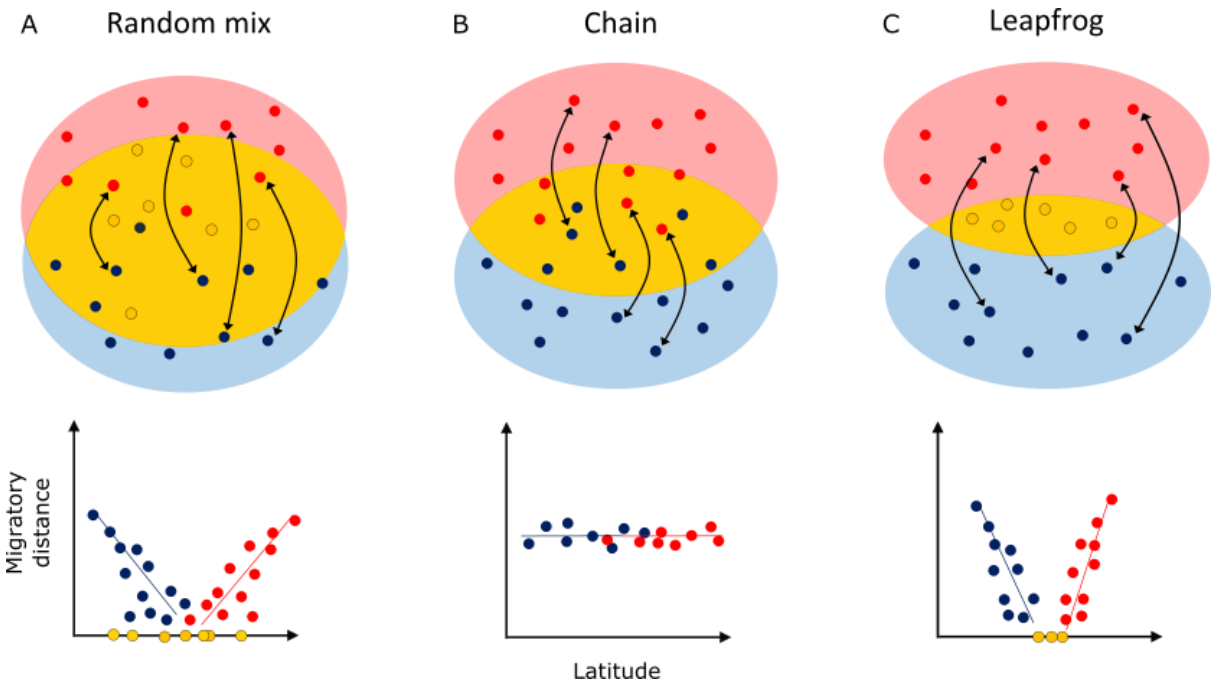

***Figure 4.1: Within-species migratory strategies and expected corresponding graphs**: migratory distance as a function of latitude; blue: winter latitude, red: summer latitude; yellow: resident individuals. A) Random mix, B) chain migration, C) leapfrog migration.*

4.3.2. Application to 9 North American birds

Newton (2008) recommended that understanding "how common these different patterns of latitudinal segregation are among migrants, or whether they differ in frequency between regions" should involve "comprehensive widescale analyses of ring recoveries", and that is what I do here. I analysed the North American ringing scheme (USGS Bird Banding Laboratory. 2016) because it covers a continent-wide territory within which many species

migrate. The program has been ringing birds in the United States and Canada since the early 20th Century. The data collated under this scheme contains the location and date of ringing of each individual bird, as well as (if applicable) any subsequent re-sights, along with other information that was not used in this study.

4.3.2.1. Species data

I focused on 9 land bird species for which there was a reasonably high number of records spanning most of their breeding and of the non-breeding ranges (Table 4.1). I defined breeding season locations as those recorded between June and August, and non-breeding season locations as those between December and February. I then searched for individual birds such that there was at least one location from each season. When several recoveries were available for a given individual, I used the first record only (the closest in time to the ringing event). I excluded recoveries of dead birds, as there can be mismatches between the re-sighting dates and the date the birds were in the area and died.

I also checked that for each species, and for each season, the distribution of records used in the analysis was broadly representative of the whole distribution of the species, as assessed by visually comparing the distribution of the specific records analysed with the (much larger) dataset of all locations (ringings and recoveries) for the same species in the same season. I found no large gaps in the distribution of records analysed, and so no evidence of populations being captured by the ringing scheme during one season only (which would have implied that they migrate, in the opposite season to regions with few observers, see Figure B1 for details).

For visualisation of the species' data, I present for each of these 9 species three maps of the respective migration patterns, each map providing different insights:

1) The species' ranges (extent of occurrence) as mapped by BirdLife International & NatureServe (2016), distinguishing resident, breeding and non-breeding ranges (Figure 4.2). These correspond to the most common form of representation of migration patterns at the broad species level. They show substantial variation in their extent (e.g. Eastern North America only for the Common grackle, vs. across the continent for the American goldfinch or the Evening grosbeak), as well as in the extent of the 'resident range' alone (e.g. a considerable part of the overall range for the American goldfinch or the Common grackle, vs. a very narrow band for the Purple finch).

2) Migration trajectories, plotted as lines linking each pair of locations (one per season) belonging to the same individual (Figure 4.3). This illustrates the migratory connectivity of populations within species, as well as representing the preferential direction(s) of migration.

3) Seasonal presence, distinguishing points that correspond to residents (as defined for the purposes of Test 2, i.e. a latitudinal span lower than 0.5 degrees), and points corresponding to breeding and non-breeding locations (Figure 4.4A).

***Table 4.1: List of species under study**, with some of their characteristics and the number of individuals in the final dataset (only locations with reasonable leverage)*

Common name	**Latin name**	**Habitat**	**Final number of individuals**	**Final number of migrants**
American goldfinch	*Spinus tristis*	Open woodland	84	30
American robin	*Turdus migratorius*	Open woodland	227	181
Brown-headed cowbird	*Molothrus ater*	Grassland	522	98
Common grackle	*Quiscalus quiscula*	Open woodland	243	225
European starling	*Sturnus vulgaris*	Town	723	130
Evening grosbeak	*Coccothraustes vespertinus*	Forest	147	74
House finch	*Haemorhous mexicanus*	Town	205	160
Purple finch	*Haemorhous purpureus*	Forest	121	82
Red-winged blackbird	*Agelaius phoeniceus*	Marsh	136	42

4.3.2.2. Testing of migratory strategies

I applied to each species each of the two tests described above. I defined resident individuals as those with a migratory distance smaller than 0.5 degrees. Null models were obtained by generating 5,000 random matches of breeding and non-breeding locations. Having found in several cases contrasting results between the tests for the same species (see results), I repeated Test 1 for the migratory individuals only.

All mapping and analyses were done in R (R Core Team 2017).

4.3.3. Results

For most species, the highest proportions of resident individuals is found at central latitudes of the overall range (Figure 4.4A), which is consistent with the location of the 'resident range' (Figure 4.2). However, some species have high proportions of residents at all latitudes along the Pacific coast (e.g. European starling). The House finch has a high proportion of residents on the whole western part of its range. On the Atlantic coast, there is a tendency across multiple species for individuals in Florida to be resident (e.g. Common grackle, Red-winged blackbird). I also note a certain level of mismatch between species- and individual- level patterns (Figure 4.2 vs. Figure 4.4A), with areas belonging to the 'resident range' containing several migratory individuals (e.g. western part of the range of the House finch, south of the resident range for the Common grackle).

In general, most species follow a simple structure of migration, with individuals following broadly parallel north-south migration directions (somewhat funnelling southwards, following the continental shape, Figure 4.3). However, some species also show more complex migration structures. For instance, some individual Purple finches and Evening grosbeaks migrate in an extreme south-eastward direction to their winter grounds (the individuals located in the central and western-central part of the range, Figure 4.3), which contrasts with the other individuals following more of a southward journey to their non-breeding range. Another divergence from the common southward migration towards the non-breeding range can be observed in the House Finch, for which some individuals undertake east-west journeys between seasons.

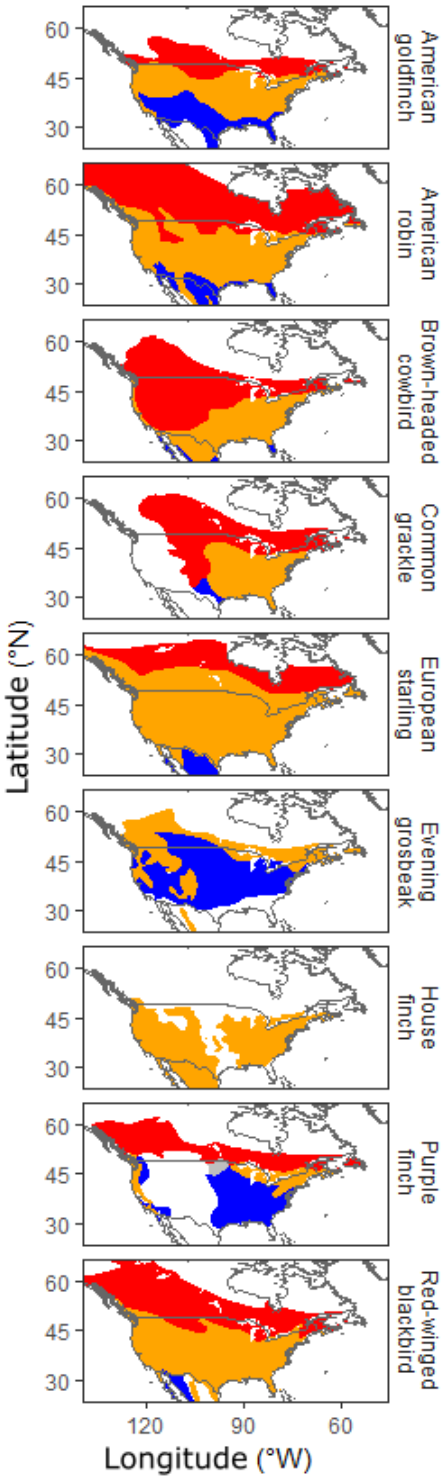

Figure 4.2: Species ranges as provided by the International Union for the Conservation of Nature*; red: breeding range, blue: wintering range, orange: resident range, grey: zone of passage on migration.*

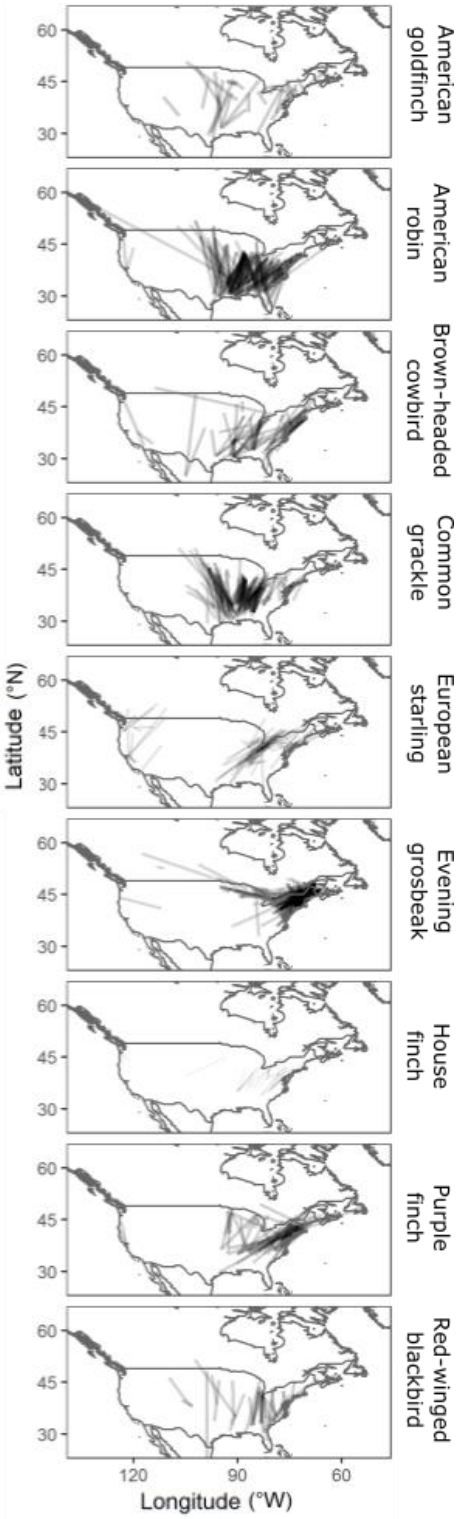

Figure 4.3: Migratory connectivity between different parts of the ranges*: black lines join pairs of winter-summer locations for each individual.*

Resident and migrant individuals seemed to follow different strategies. Indeed, for most species residents are spread all over the latitudinal range (Figure 4.4A), and are more numerous in the resident range than would be expected by chance (Figure 4.3C). Even when there seems to be a pattern in the relationship between latitude and migratory distance, residents do not fall at all along the lines where they would be expected to be, causing the PCA axis to badly capture the data in Test 1 (Figure 4.3B). Results for Test 1 with all data and for Test 2 conflicted for most species (Table 4.2). All the above justified the exclusion of residents for the final Test 1.

All species show a V-shaped migratory pattern (Figure 4.4B-C), with no species showing a steep pattern typical of leapfrog migration (Table 4.2, Test 1 without residents). Most species did not deviate from the expectations under random mixing (Table 4.2, Test 1 without migrants), but the patterns for the Brown-headed cowbird and the European starling are shallower than the null expectation, suggesting some degree of chain migration. The details of the random distributions of slopes can be found in Figure B3 to Figure B6.

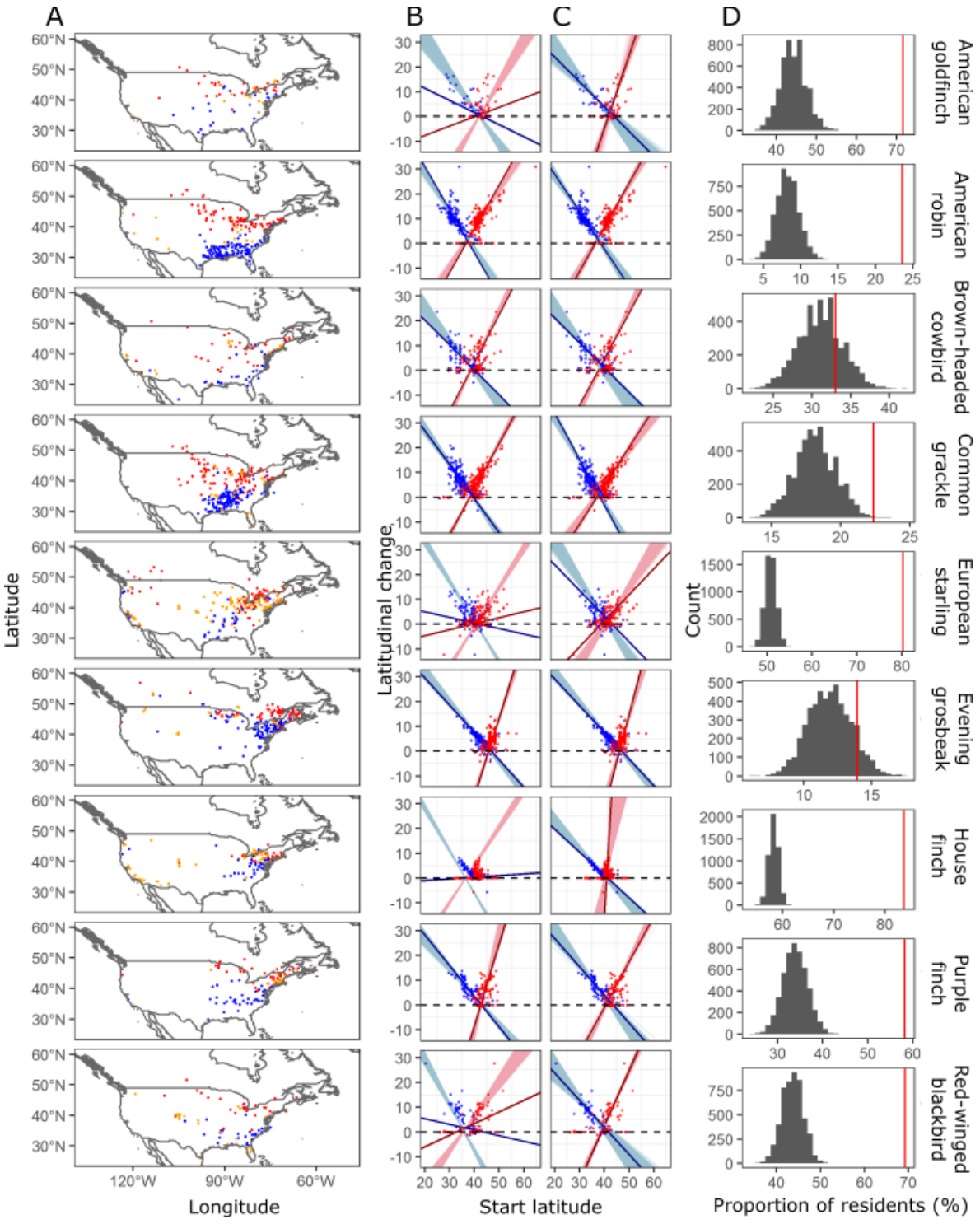

Figure 4.4: Spatial patterns and results of the test for each species. *A: Distribution of summer migrants (red), winter migrants (blue) and residents (yellow); B and C: results for test 1 (B: all individuals included, C: migrants only), points: empirical data, lines: 1st axis of the PCAs (dark: empirical data, light: randomisations) for summer (red) and winter (blue) locations. D: results for test 2: distribution of the proportions of residents in the 'resident range' under the null model (histograms) compared with the empirical data (red line).*

Table 4.2: Results of the tests *(**: outside of the 99% CI; *: outside of the 95% CI)*

Species	**Test 1 - all data**	**Test 1 - migrants only**	**Test 2**
American goldfinch	Chain-like **	Random mix	Leapfrog-like **
American robin	Leapfrog-like *	Random mix	Leapfrog-like **
Brown-headed cowbird	Chain-like **	Chain-like **	Random mix
Common grackle	Random-mix	Random mix	Leapfrog-like *
European starling	Chain-like **	Chain-like **	Leapfrog-like **
Evening grosbeak	Winter: chain-like *, summer: leapfrog-like *	Random mix	Random mix
House finch	Chain-like **	Winter: chain-like **, summer: leapfrog-like **	Leapfrog-like **
Purple finch	Random mix	Random mix	Leapfrog-like **
Red-winged blackbird	Chain-like **	Random mix	Leapfrog-like **

There is also one species, the House finch, showing an unexpected, incoherent pattern: the winter V leg is more horizontal than random (compatible with chain migration), but the summer leg is more vertical (compatible with leapfrog migration). A detailed look at the summer leg shows that the line is close to vertical, indicating no relationship between distance and latitude (thus also incompatible with a leapfrog strategy). This pattern is a result of the lack of long-distance migrants (i.e. individuals migrating as far as they could while still remaining within their species' range) in the empirical data. Some long-distance migrants appear by chance in the randomisations. Due to geographical constraints, these long-distance migrants are located in the south of the non-breeding range, and in the north of the breeding range. Their effect then depends on the relative width of the ranges: the winter range is relatively latitudinally wide, so individuals in the south migrating longer distances drive the lines for the randomisations to be steeper in that season. In contrast, the nearly-vertical line created by the relative latitudinal narrowness of the summer range is made oblique in the randomisations because of long-distance migrants appearing in the northern part of the range. I consider this incoherent pattern as a limit case where my test does not allow to conclude for any of the strategies.

4.4. Discussion

Here I present an overview of within-species differences in migratory strategies for nine passerine and near-passerine species breeding and wintering in North America. I present a formal test to categorise within-species migratory strategies that I apply to these species.

4.4.1. Migrants vs. residents

One striking pattern that emerges from these tests is the fact that resident individuals seem to follow a completely different strategy from the migrants. One potential explanation for this result is that the costs of remaining resident differ between individuals. First, some physiological differences can exist between individuals that make them better suited for one or the other strategy. For instance, Nilsson et al. (2011) found in blue tits that the basal metabolic rate was lower in migrants than in residents, and that the energetic cost of thermoregulation was lower in resident males compared with females and all migrant individuals (allowing them to suffer less from the harsh winter climate). Second, dominance can also differ between migrants and residents, with dominant individuals more likely to be better competitors for food when resources become scarce (Sekercioglu 2010). Additionally, not moving at all can present several advantages over even very short migrations. Indeed, being resident means keeping one's territory all year round and being on the breeding range before all the migrant individuals, providing a competitive advantage for controlling the best territories (Sekercioglu 2010). Thus, the trade-offs experienced by migrants and residents might differ significantly.

We can gain insights in the factors that favour residency by looking at the distribution of resident individuals. As shown in Figure 4.4, some areas seem to have high concentrations of residents. For instance, in several species, individuals in Florida tend to be resident (Common grackle, Red-winged blackbird, Figure 4.4). Some species also contain mostly residents along the Pacific coast of the US and Canada (American crow, House finch and, to some extent, European starling, Figure 4.4), and high concentrations of residents can be found in areas of high human population density (Figure 4.4 and Figure B7). However, more ringing/recovery effort somewhere should affect both migrants and residents in the same way. Two potential biological explanations can be raised. First, urban areas may have more year-round resources, for example because of bird feeders (Plummer et al. 2015), garbage (Gilbert et al. 2016), or irrigation in dry areas. Second, the location of urban areas could also be biased towards areas with relatively stable environmental conditions that favour the establishment of residents.

Additionally, some patterns of residents' distributions can also be understood, in part, with historical insights. For example, the eastern House finch population was introduced from Southern California, where the species is resident, and became progressively migratory (Able and Belthoff 1998). There are thus multiple reasons to treat residents and migrants separately.

4.4.2. High degree of randomness

Six out of nine species do not deviate from a random mix, with only two species showing evidence for chain-like migration (and none following a leapfrog strategy). And it is not only latitudinal patterns that fail to follow one of the strategies defined by Newton (2008), longitudinal patterns also present aspects of random mixing. First, migrants tend to keep similar longitudes in both ranges (Figure 4.3), which can be seen as a way to minimise the migration distance that allows to reach regions characterised by similar environmental conditions or providing enough resources. For some species, additionally, migratory distance tends to increase at intermediate longitudes (i.e. individuals breeding further west tend to winter in more central regions, Figure 4.3). This also appears for the American crow and the Common grackle in the vertical line in Figure 4.4, representing individuals occupying a wide range of longitudes during the breeding season and concentrating in a smaller area (smaller range of longitudes) during the non-breeding season. This pattern can be linked with the presence of mountains south of the breeding ranges of these individuals, which constrain the areas where birds can fly to winter. However, not all species follow a longitudinally structured migratory pattern. In particular, the Purple finch and the Evening grosbeak follow messier patterns (Figure 4.3), with some individuals further east during the breeding season migrating to locations further west and conversely, a pattern that had previously been described as 'irruptive migration' (e.g. Bock and Lepthien 1976 for Evening grosbeaks). Therefore, both latitudinal and longitudinal patterns contain a certain degree of apparent randomness.

4.4.2.1. Reasons for randomness

The apparent randomness in individual destinations found in many species might underline strong inter-individual differences which were not accounted for in this study. For example, body condition can influence how far individuals migrate, with individuals in better condition able to cope with longer-distance migrations. Age or sex can also influence how far individuals migrate (e.g. females White-throated sparrow *Zonotrichia albicollis* have been found to migrate further than males; Jenkins & Cristol 2002). Personality has also been found to influence bird

movements (Patrick and Weimerskirch 2014), therefore it could potentially also have an effect on how far individuals migrate. All of these mechanisms can make migratory decisions appear random at the individual level if these factors are not corrected for, but are likely to be averaged at the species level.

Whilst the lack of a consistent individual strategy might be the result of intrinsic individual differences, a biased distribution of observers could also limit my ability to detect migratory strategies. My dataset is a collation of all ringing efforts throughout North America, and thus does not represent a systematic sampling of the region. To reduce observer bias, I focussed on species with ranges fully within North America, as ringing effort is comparatively limited in South America. However, even within North America, there might still be heterogeneities in the density of observers (due to accessibility or socio-economic factors). For this reason, I checked that the distribution of my ringing records provides a good representation of the full range of the species of interest. Whilst this requirement, together with my stringent limit on the minimum number of records, restricts the number of species that can be investigated, it should minimise the possible role of observer bias in my study.

Finally, issues related with time are another source of potential additional noise. First, my definition of breeding and non-breeding season can be seen as crude. In order to have a criterion that I could use similarly for all species, and that would be a good compromise between the number of data points and the risk to include birds that have not completed their migratory journey yet, I considered June to August as the breeding season and December to February as the non-breeding season. However, there might be variations between and within species in arrival and departure dates (e.g. between-species variation: American Goldfinches tend to be late breeders, whereas Brown-headed cowbirds, as most brood parasites, tend to leave the breeding grounds earlier than other birds, sometimes even in late July, Ortega 1998; within-species variation: adult European starlings arrive earlier and leave later the breeding ground than juveniles, Feare, in Wernham et al. 2002). Second, as I only have access to two (not necessarily consecutive) sightings per individual, I do not take into account potential changes in migratory strategies between years. However, partial migration can be facultative (i.e. individuals skip migration some years but not others). For example, some environmental conditions (e.g. poor food availability) can trigger migration (e.g. in Tropical Kingbird populations of the southern Amazon Basin, a dramatic dry season decreasing the abundance of insect food can promote migration of some individuals, Jahn et al. 2010). It is thus possible that

I captured migratory decisions that correspond to years with very different environmental conditions.

4.4.3. Textbook patterns

Despite these limitations, some chain-like patterns still emerge from my tests. Chain migration could suggest some degree of individual specialisation, with individuals preferring warmer environments, for example, staying in the most southern part of both the breeding and the non-breeding range. More simply, it could also mean that there is a limit to how far individuals are willing to migrate, so the most northern areas of the breeding range, for example, cannot be occupied by individuals wintering the furthest south.

I did not detect any instance of leapfrog migration. This might be a consequence of the high spatial overlap of the breeding and non-breeding ranges for most species in my study. If the summer and winter ranges overlap much (i.e. the 'resident range' is very wide), there is little potential for leapfrog migration, as this pattern requires residents to be in the overlapping part of the breeding and non-breeding ranges, as any individual breeding north of the residents would migrate over them to reach non-breeding grounds south of the residents. On the contrary, even if ranges overlap a lot, there is still scope for chain migration, and this would just mean that in the overlapping part of the ranges, winter migrants will replace summer migrants and vice versa. This is true even when not considering resident individuals (as discussed above, residents might follow different rules).

Examples of species following leapfrog or chain strategies are widespread in the literature, but how representative are they of the range of strategies in bird species? Is there a report bias towards species that follow these clear patterns? My study would suggest this is the case, as in my sample of 9 species migrating within North America, a high proportion follow strategies that do not deviate from the null expectation. However, I should point out that my sample of species is biased towards widespread, abundant species in North America (for which there are good ringing records), and they all are passerines and near-passerine. Leapfrog and chain migration might be more widespread in different taxa, such as waterfowls which are geographically more constrained, or in other regions with different environmental conditions.

Overall, I here argue that it is important to quantitatively test for migratory patterns using extensive individual-level data. Although the IUCN range maps have proven very valuable to investigate the spatial ecology of migratory species, they do not provide information about

connectivity within the range, which has important implications for disease spread and conservation strategies. I therefore advocate using ringing data with the tests developed in this chapter to a better understanding of the spatial ecology of these species. My application of these methods emphasises the magnitude of within-species variability in migratory distances, raising the question why individuals have such different strategies and what can be driving these inter-individual differences.

5. The costs and benefits of migration: the role of temperature, resources and migratory distance on individual strategies

5.1. Abstract

A number of hypotheses have been raised to explain what drives animal seasonal migrations, all based on different benefits (e.g. tracking of resources and climate niche) and costs (e.g. distance travelled). Although, ultimately, individuals are the ones making movement decisions, these hypotheses have been tested at the species level, but not using data on individual movements. Here, I use ringing/recovery data on nine North American bird species to present results consistent with the hypothesis that migration allows individuals to better track their climatic niche, and that it increases their access to resources compared with staying resident. I then present results suggesting that, as was found at the species level, individuals trade off these benefits against the cost of migratory distance. Finally, I quantify how individuals perform in this trade-off compared with their available options and present results indicating that migratory distance is actually the main driver of the choice of migratory location.

5.2. Introduction

Migration, the seasonal redistribution of individuals between breeding and non-breeding grounds, is widespread among birds (Greenberg and Marra 2005). Because migratory bird species have two separate geographical ranges, they are faced with choices to make regarding how to redistribute within the ranges between the two seasons, with environmental conditions in one part of the range affecting species throughout their range. Migration therefore acts as a 'natural experiment', allowing us to get insight into what drives the choices of breeding and non-breeding locations (Somveille et al. 2015). However, although several previous studies aiming at understanding the ecological mechanisms of migration (e.g. Somveille et al. 2015, Hurlbert and Haskell 2003, Boucher-Lalonde 2014) have focused at the species level, ultimately individuals are the ones making movement decisions, with the species' seasonal ranges then emerging from the sum of these decisions. Valuable insights can therefore be obtained from the study of individual migratory decisions regarding their spatial location during the breeding and non-breeding seasons (throughout, I use the term "migratory decisions" in this strict sense).

The results of previous macroecological studies (Nakazawa et al. 2004, Somveille et al. 2015, Gómez et al. 2016, the previous chapter in this thesis) suggest three key factors that might affect migratory decisions in birds. First, migration may allow individuals to track their niche throughout the year. Indeed, assuming that individuals/species are adapted to certain environmental conditions, migration could allow them to follow these conditions from one season to the next (e.g. Somveille et al. 2015, Gómez et al. 2016). Supporting this hypothesis, Gómez et al. (2016) found in New World warblers that migratory species track their climatic niche better than resident species. At the individual level, Ramos et al. 2015 found evidence for individual specialisation in Bulwer's petrels *Bulweria bulwerii* migrating between the North and South Atlantic, as populations leapfrog each other during migration to find conditions in the non-breeding season that are similar to the ones they experience in the breeding season. In Chapter 4, I found that some species of North American passerines and near passerines follow chain-like migration patterns, which, for migrations within the same hemisphere, also suggests a degree of individual specialisation (with individuals that prefer colder temperatures staying in the northern part of both the winter and the summer species ranges, and individuals preferring warmer temperature staying in the southern part of the ranges). However, in most species I analysed (7 out of 9) I did not find evidence that individuals are following a clear latitudinal migratory structure, instead appearing to redistribute latitudinally randomly.

Second, migration may allow individuals to maximise their resource gain throughout the year. This aspect is mainly linked to seasonality in resource availability at different locations. Indeed, at any given location, residents are limited by the amount of resources that can be found year-round; but if one season is more productive than the other, then it has a surplus of resources that will be available to migrants (Herrera 1978). Hurlbert and Haskell (2003) provided support for this hypothesis by finding that the seasonality in resources (as measured by the Normalized Difference Vegetation Index, NDVI) explained 61% of the spatial variation in migratory avian species richness in the United States. Dalby et al. (2014) were able to explain a good part of the latitudinal gradient in waterfowl species richness during the breeding season using seasonal variability in plant productivity. In particular, they found that annual plant productivity and evapotranspiration explained very little of the gradient, but intra-annual variability explained more of it, emphasizing the importance of seasonality. Thorup et al. (2017) found that Common cuckoos *Cuculus canorus* appear to maximise the vegetation greenness they experience by migrating, whereas Red-backed shrikes *Lanius collurio* and Nightingales *Luscinia megarhynchos* track seasonal surplus in greenness. All these studies suggest that access to resources is important in migratory decisions.

Third, distance may be highly costly for individual migrations, through energetic cost (e.g. Wikelski et al. 2003) or increased mortality risks (Newton 2008), including weather-induced starvation, in-flight losses (see Newton 2007 for a review of weather-related mass mortality events in migrants), and risks associated with anthropogenic structures, such as artificial lights or powerlines (Newton, 2008). If so, any advantages of migration (niche tracking and/or maximised resource gain) should be balanced against the costs of migration. I should therefore expect a trade-off between migratory distance and how well individuals track their niche or reach energetically advantageous locations. Somveille (2015, Chap. 4) found such a trade-off at the species level for resource gain. However, for thermal niche tracking, the relationship was not linear, with thermal distance (difference between breeding and non-breeding temperature) initially decreasing with migratory distance, but eventually increasing.

Fourth, if such a trade-off exists between the cost of migratory distance and the benefits of migration in terms of niche tracking and resource gain, we can wonder how individuals actually perform along that trade-off. At the species level, Somveille (2015, Chap. 4) found that species tend to select migratory strategies that allow them a better access to resources, a better tracking of thermal conditions, and a shorter distance travelled compared with available options, thus

balancing the three factors simultaneously. But I do not know whether, at the individual level, these three factors are also given equal importance, or if some are prioritised.

These hypotheses can be tested using individual migratory data. Such individual data are increasingly made available, either with high resolution but low sample size data (e.g. tracking data) or with lower resolution but high sample size and spatial coverage data (e.g. ringing data). Here I take advantage of a large-scale ringing/recovery dataset (from the Bird Banding Lab) for nine species across North America, to answer the following questions about drivers of individual bird migrations: 1) Does migration favour thermal niche tracking and access to resources when compared to residency? 2) Are these benefits traded off against the cost of migratory distance? 3) How do individuals perform along that trade-off in comparison to alternative migration options?

5.3. Methods

5.3.1. Data

5.3.1.1. Individual locations

I used data from the North American ringing scheme (USGS Bird Banding Laboratory, 2016), which contains, for each bird, locations (i.e. longitude and latitude) and dates of ringing and re-sightings. I selected nine species of passerines and near passerines: the American crow (*Corvus brachyrhynchos*), the American goldfinch (*Spinus tristis*), the American robin (*Turdus migratorius*), the Brown-headed cowbird (*Molothrus ater*), the Common grackle (*Quiscalus quiscula*), the European starling (*Sturnus vulgaris*), the Evening grosbeak (*Coccothraustes vespertinus*), the House finch (*Haemorhous mexicanus*), the Pine siskin (*Spinus pinus*), the Purple finch (*Haemorhous purpureus*), and the Red-winged blackbird (*Agelaius phoeniceus*). See Chapter 4 for a description of species and data selection, and Fig. C2 for the distribution of records in time.

As in Chapter 4, I defined summer (corresponding to the breeding season) as the months of June to August, and winter (corresponding to the non-breeding season) as the months of December to February. I constrained the definition of the seasons to reduce the odds of records corresponding to birds in migration. I retained only individuals for which I had a location in each season. For each species, I thus have a variable number of individuals, with a pair of

observations (summer and winter) per individual. For each individual, migratory distances were calculated as the great circle distance between these two locations. In order to focus only on migratory strategies, I removed resident individuals (defined as individuals moving less than 50 km from one season to the next, see Chapter 4 in this thesis) from the dataset.

5.3.1.2. Environmental data

Temperature has been found to play a role in driving bird migration, either as a limit to what is tolerable by a species (migratory birds avoid regions with very cold winters; Somveille et al. 2015), or as migratory species track temperature between seasons (e.g. in warblers, Gómez et al. 2016). I thus used seasonal mean temperature to characterise individuals' thermal niche. I calculated monthly means from the Worldclim database (resolution 30''; Hijmans et al. 2005), further aggregated to seasonal means using the same definition of summer (June to August) and winter (December to February) as used to classify the ringing locations. I then calculated, for each individual, temperature range as the absolute value of the difference between the mean winter temperature (at the winter location) and the mean summer temperature (at the summer location).

As an indicator of resources (food, nesting sites and roosting sites), and following Hurlbert and Haskell (2003), and Somveille et al. (2015), I used the NDVI (Normalized Difference Vegetation Index), a remote sensing index of greenness, that can be related to the amount and type of vegetation present: positive values of NDVI correspond to vegetated areas, and higher NDVI values tend to be interpreted as healthier and denser vegetation (Jackson and Huete 1991). I used monthly averages from NASA's Earth Observatory (resolution 0.1°; available from https://neo.sci.gsfc.nasa.gov/). To obtain representative values, I computed monthly means over 2006-2015 and, from those, seasonal means following the same approach as for temperature data.

I calculated the energetic gain (seasonal surplus in resources from one season to the next) at each location in each season as in Somveille et al. (2015):

$$Gain_{location \in season1} = NDVI^{season1}_{location \in season1} - NDVI^{season2}_{location \in season1}$$

I obtained a value of year-round resource surplus per individual by summing the gains for the respective pair of locations in the corresponding seasons. By definition, a resident individual would have a total annual gain of 0. A positive value means that migration allows individuals to get access to more resources than if they had been resident, a negative value means that migration makes individuals get access to less resources than residency.

The environmental data that I used corresponds to seasonal means over multiple years, hence not capturing the interannual variability in conditions. Even though there are reconstructions in time of climatic data (e.g. NOAA-CIRES 20th Century Reanalysis, available at http://www.esrl.noaa.gov/psd/), to my knowledge, such reconstructed data are not available for NDVI data. To obtain comparable results, I used seasonal means both for measures of the climatic niche and of resource surplus.

5.3.2. Analyses

I asked three main questions about the drivers of individual migration for the nine species in my dataset. Each species was analysed separately for each question.

5.3.2.1. Question 1: What are the benefits of migration compared with residency?

I tested whether migration allows individuals to better track their climatic niche than if they were staying, by comparing the inter-seasonal temperature range experienced by migrants with the temperature range they would experience if they were residents instead, by remaining either at their non-breeding or at their breeding location. If so, then the temperature range should be smaller for the migrant strategies than for the resident strategies.

I tested whether migration allows individuals to increase access to resources compared with staying, by comparing their year-round resource surplus with 0 (the value for residents). If so, the year-round resource surplus should be higher than 0.

5.3.2.2. Question 2: Are the benefits of migration traded off against the costs of travel distance?

To investigate whether there is a trade-off between migratory distance and the two above-described benefits of migration, I tested the relationship between migratory distance and 1) temperature range between summer and winter, or 2) total annual energetic gain, by fitting a different linear model for each species. If there are such trade-offs, I expect a negative relationship between temperature range and geographical distance, and a positive relationship between energetic gain and geographical distance.

5.3.2.3. Question 3: How do individual migratory strategies perform regarding each cost/benefit in comparison with alternative options?

I investigated this question by comparing each individual with virtual individuals, adapting to the individual level the approach that Somveille et al (*in review*) developed at the species-level.

The performance of individual strategies was quantified in terms of: 1) temperature range (the narrower the range, the higher the benefit of migration in terms of niche-tracking); 2) resource scarcity (1 – standardised year-round resource surplus; the lower the scarcity, the higher the benefit of migration in terms of access to resources); and 3) distance (the shorter the distance, the smaller the cost of migration). The performance of a migratory strategy here is a measure of the extent to which this strategy minimises the costs/maximises the benefits mentioned above. For each of these costs/benefits, high performances correspond to low values.

For each individual, I generated virtual individuals by taking one of the observed locations of the individual (winter or summer) and one randomly generated point corresponding to the other season (see below for more details). A virtual individual corresponds to a theoretical alternative migratory option, whose performance can also be measured along each of the three axes above.

For each individual, and for each performance component, I quantified the performance of the observed migration by analysing its rank among the alternative migratory options. I obtained a score between 0 and 1, where 0 means that the observed migration is better than all the alternatives tested, 1 means that it is worse, and 0.5 means that it falls in the middle.

If individuals' migratory decisions (i.e., selection of breeding and non-breeding locations) are driven by maximising niche-tracking, by maximising access to resources, or by minimising migration costs, I expect that most individuals in any given species should have a relatively high performance, i.e., relatively low ranks, for the corresponding component. This should translate into a distribution of ranks that is right-skewed (i.e. with a long tail on the right side).

For each species, I tested this hypothesis at two geographical scales – within the species' range; and at the continental scale – by applying two methods for generating the randomly located destinations of virtual individuals.

To test this effect within the species range, I generated each virtual individual by taking the species' observed location in a given season (summer or winter) and the location of any of the individuals of the same species in the opposite season, constrained to go south in the winter and north in the summer. This analysis thus assumes that realistic migratory alternatives for any given individual must remain within the species' range.

At the continental scale, I assumed instead that any individual could potentially migrate to any location in North America between 20˚N and 75 ˚N (excluding islands and the Yutacan peninsula, because flying there would imply the higher costs of flying over seas), also

constrained to go south in the winter and north in the summer. I generated alternative destinations by using a hexagonal grid (ISEA discrete global grid, resolution 7, hexagon area ~ 23,375 km^2, available at http://bufo.geo.orst.edu/tc/firma/gg/table.html) covering the study area. Both the observed and the possible alternative locations were characterised based on these hexagons: temperature and NDVI as the mean values across the pixels overlapped per hexagon; locations (for calculating distance) assumed to be the centroids of hexagons.

The number of virtual individuals generated in each case was variable: in the analysis within the species' range, it depended on the total number of individuals of the same species in the database; in the continental-scale analysis, it depended on the number of hexagons. In both cases, one virtual individual was generated for each of the available alternatives satisfying the condition on the directionality of migration (going south in winter, going north in summer). To avoid an imbalance towards one season, the same number of virtual individuals was generated in both cases: for the season with the smallest number of alternatives, all were considered; for the other season, a random sub-sample (of the same size as for the other season) was considered.

5.4. Results

5.4.1. Question 1: What are the benefits of migration compared with residency?

For all species, the temperature range between summer and winter is significantly narrower when individuals migrate than it would be if they stayed either at their winter or at their summer location (Figure 5.1), consistent with the hypothesis that migration allows individuals to better track their climatic niche. In all cases, staying at the summer location year-round leads to a greater inter-seasonal temperature range than staying at the winter location year round (Figure 5.1).

I found that for all species, all or nearly all individuals experience a surplus in resources at their summer location (i.e. this location holds more resources in summer than in winter) and a deficit in resources at their winter location (i.e. there are less resources at this location in the winter than in the summer; Figure 5.2). However, how advantageous migration is in terms of total resource gain depends on the species. For most species, there is on average a positive resource gain (Figure 5.2), consistent with the hypothesis that migration allows individuals to increase access to resources. However, for several of these species, there is a high number of individuals for which migration actually leads to a net deficit in resources throughout the year compared with being resident (e.g. Evening grosbeak, Brown-headed cowbird, European starling, House

finch). Additionally, the average population total annual gain for the House finch is not significantly higher than zero.

5.4.2. Question 2: Are the benefits of migration traded off against the costs of travel distance?

For all species, the inter-seasonal temperature range tends to decrease when the geographical distance increases (individuals migrating further tend to track their niche better; Figure 5.3), consistent with the hypothesis of a trade-off between a benefit of migration for tracking the climatic niche and the costs of travel distance. Similarly, the resource gain tends to increase with the geographical distance (Figure 5.4), consistent with the hypothesis of a trade-off between a benefit of migration for increasing access to resources and the costs of travel distance. However, even though all slopes for the relationship between distance and resource gain are significantly different from zero apart from the one for the Evening grosbeak, the proportion of variance explained by these relationships (R^2) varies greatly between species (Figure 5.4) and is consistently lower than the R^2 of the relationships between distance and temperature range (Figure 5.3).

5.4.3. Question 3: How do individuals perform along this trade-off in comparison with alternative options?

When the performance of individuals is compared with that of alternatives within the species range, ranks in terms of temperature range and resource scarcity do not significantly differ from 0.5 (Figure 5.5), which does not support the hypothesis that individual migration decisions options maximise thermal niche tracking or access to resources. I found evidence for selection for smaller geographic distance for all species but the Evening grosbeak (Figure 5.5).

At the continental scale, I found evidence of a strong selection for short distances (Figure 5.5), supporting the hypothesis that migratory distances are optimised relative to alternatives. However, and contrary to predictions, ranks along the temperature range axis are significantly higher than 0.5, suggesting that individuals track their climatic niche far worse than they could, given the considered alternatives. Also, for most species, resource scarcity ranks are also significantly higher than 0.5 (all species but the American goldfinch, the American robin and the Evening grosbeak; Figure 5.5). These results thus suggest that individual favour shorter

migratory distances, even though it comes at a cost of less favourable thermal niche tracking and available resources compared to if they had travelled further.

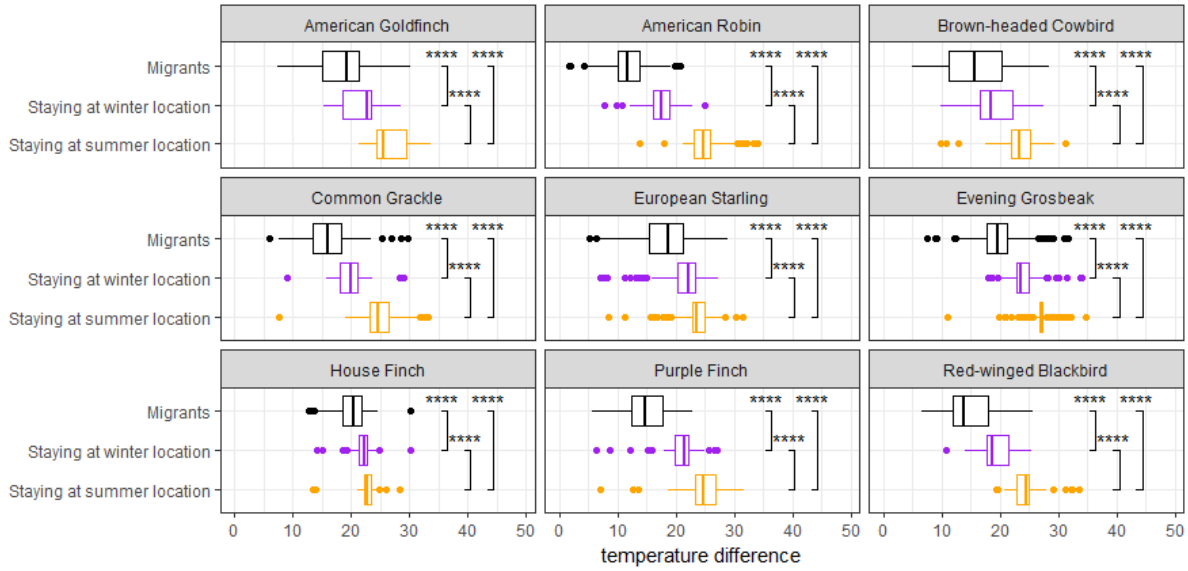

Figure 5.1: Temperature range experienced by migrants between summer and winter *(black),* ***compared with the range they would have experienced if they had stayed all year*** *at their winter location (purple) or at their summer location (orange). Indicated significance levels are for paired t-tests between each pair of conditions.*

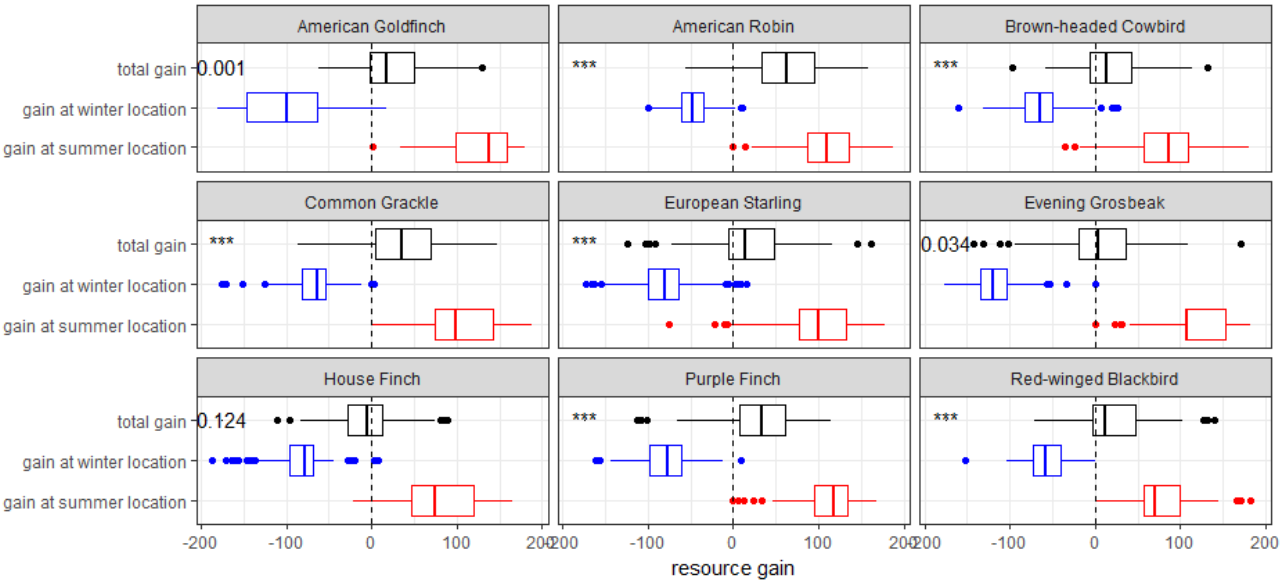

Figure 5.2: Total annual resource gain experienced by migrants and its decomposition into resource gain during summer *(summer NDVI – winter NDVI at the summer locations),* ***and resource gain during winter*** *(winter NDVI – summer NDVI at the winter locations). Significance levels for one-sample t-tests comparing the total gains with zero are also indicated.*

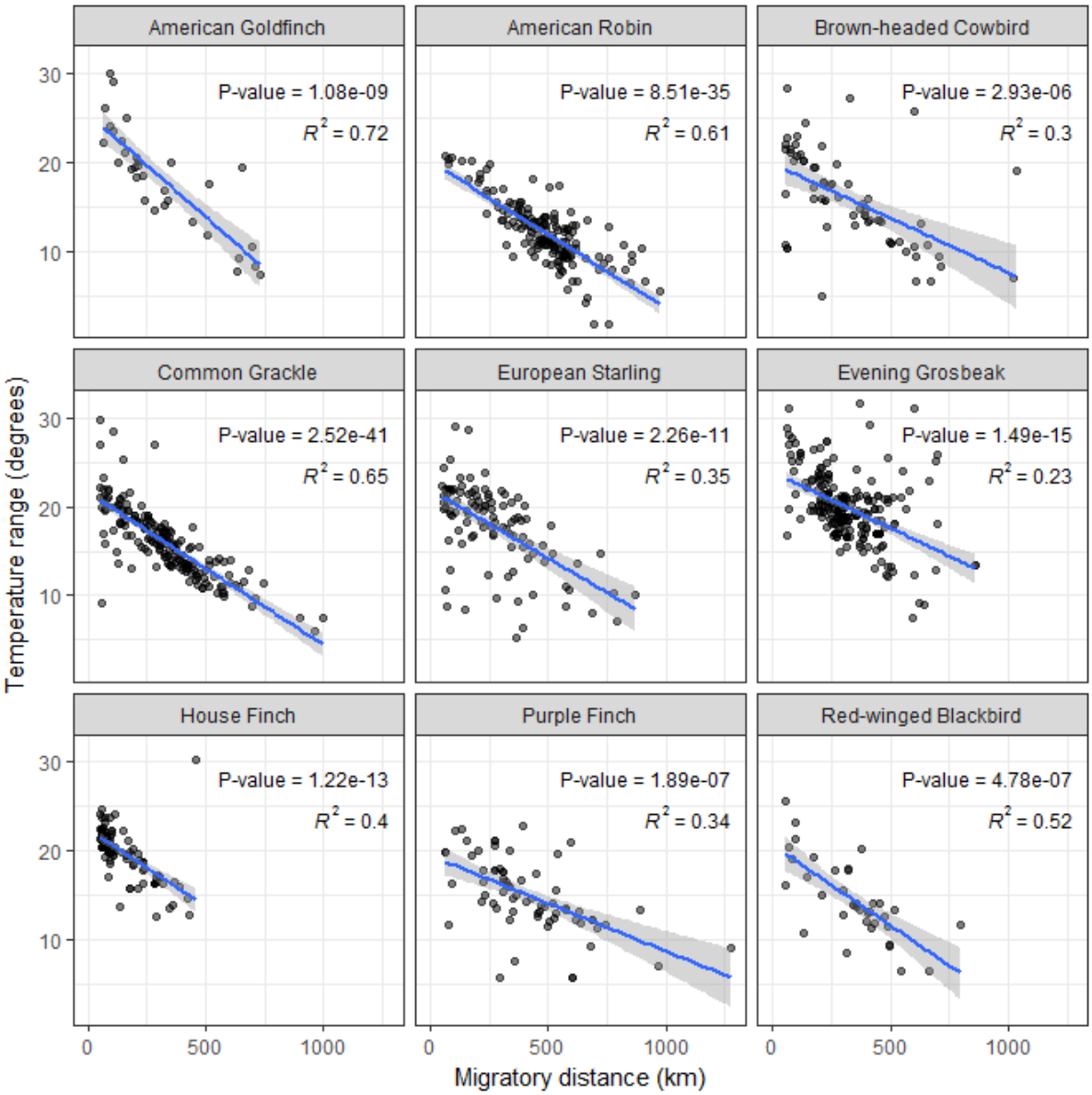

Figure 5.3: Relationship between distance travelled and temperature range between summer and winter locations, *across individuals, for each of the species analysed (data and fitted linear models).*

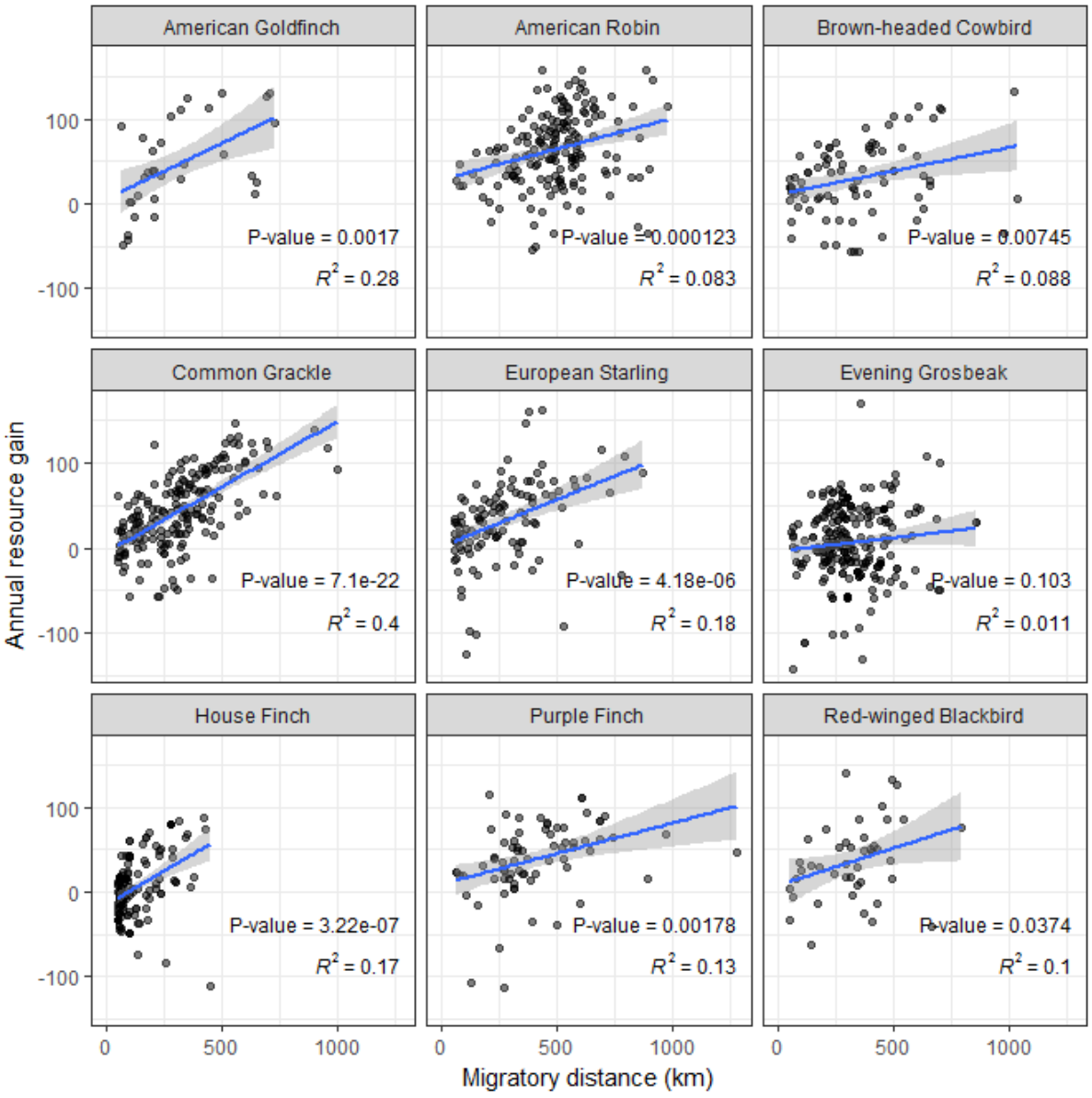

Figure 5.4: Relationship between migratory distance and annual resource gain*, across individuals, for each of the species analysed (data and fitted linear models).*

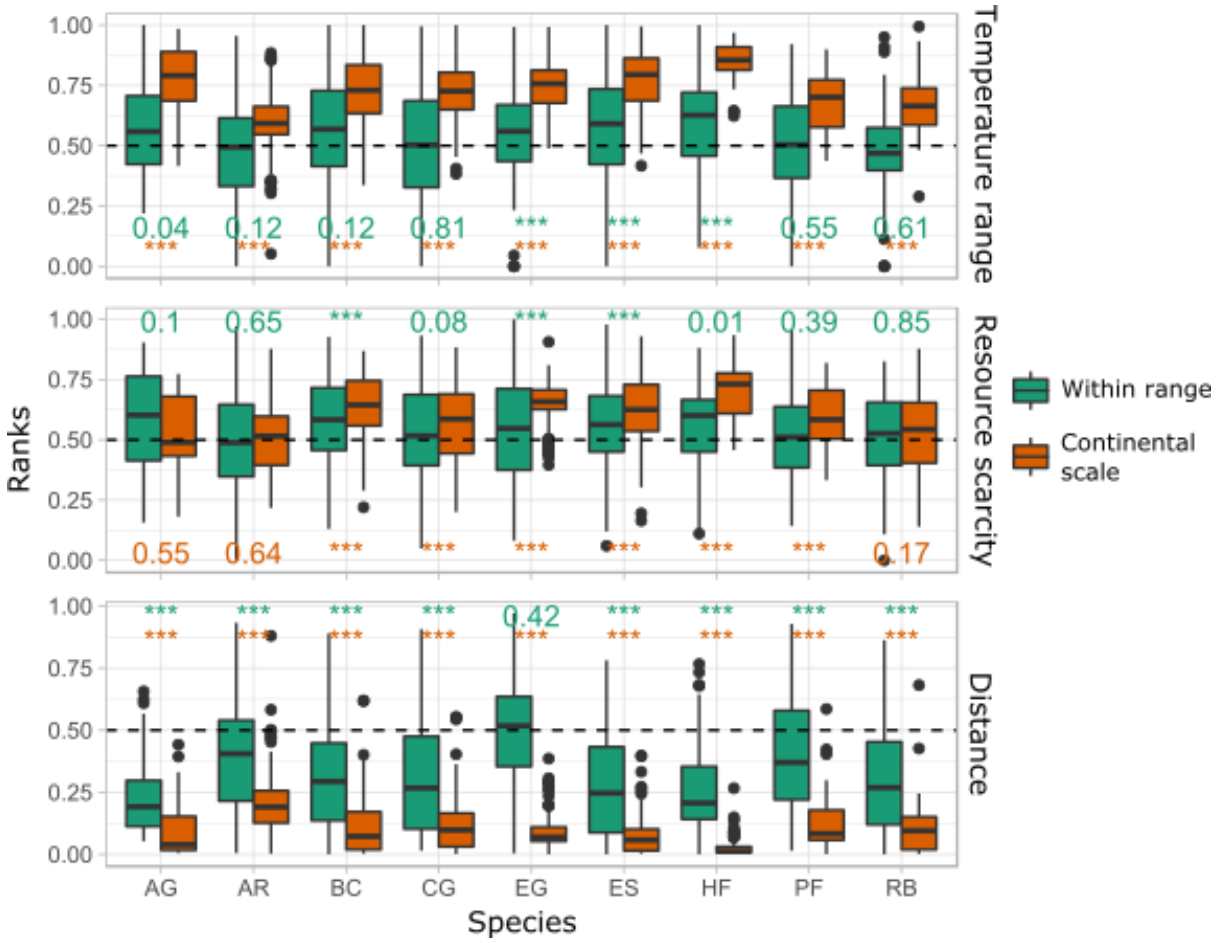

Figure 5.5: Distribution of the ranks of individual decisions for each species, each variable taken separately. *P-values correspond to one sample t-tests, comparing the empirical distribution of ranks at each scale for a given species for that variable, with a mean of 0.5.*

5.5. Discussion

My results indicate that individual birds do gain both in terms of thermal niche tracking and available resources by migrating compared to if they had stayed in the same location year around. I also found the benefits arising from thermal niche tracking increased with longer migratory distances, thus implying a trade-off between migratory costs (assumed to increase with distance) and the benefits of migration. However, when geographical constraints are taken into account, strategies only perform better, on average, than alternatives in terms of migratory distance, but not in terms of thermal niche tracking or increasing resources. In other words, individual favoured minimising the distances they had to travel, even though locations further afield would have provided higher benefits in terms of thermal niche tracking and available resources.

5.5.1. The benefits of migration (Question 1)

First, I found that by migrating, individuals reduced their between-seasons temperature range, compared with what they would have experienced by staying at their summer or winter grounds (with a stronger effect in winter). These results are consistent with findings at the species level that most species reduce their experienced temperature range by migrating (Somveille 2015, Chap. 4). Given the stronger effect in winter than in summer, it is possible that this result is driven, at least in part, by the need to avoid winter harsh temperatures (as suggested in Somveille et al. 2015).

Second, individuals in several species experience, on average, a positive resource gain, supporting the hypothesis that individuals increase their resource gain by migrating (Figure 5.2). However, for some species, individuals vary widely in whether they experience a net surplus or deficit in resources. This seems to contrast with results from Somveille (2015, Chap. 4), who found that 91% of all migratory bird species experience a net year-round surplus in NDVI. However, the species I studied here belong to the short to moderate-distance migrants, among which the results in Somveille (2015, Chap. 4) indicate that several species actually experience a net year-round deficit in NDVI.

5.5.2. Trade-offs with migratory distance (Question 2)

My results indicate that there are benefits to migrate compared with staying, but given the costs incurred by migrating, not all migratory destinations are equivalent. Indeed, the further individuals travel, the more efficient the thermal niche tracking (Figure 5.3). This suggests a trade-off between the benefits of thermal niche tracking and the cost of migratory distance. Somveille (2015, Chap. 4) found a similar effect for short to medium-distance migrants (the effect found for long-distance migrants was reverse, but none of the species in my dataset fall into this category). Additionally, the further individuals travel, the higher their gain in resources (Figure 5.4) but this relationship is much weaker than for thermal niche tracking (consistently lower R^2 for the corresponding regressions; Figure 5.4). Even among the individuals migrating long distances, several of them experience a negative total annual gain (Figure 5.4), an effect that was also found when comparing migrating with not migrating (question 1; Figure 5.2).

This suggests that either some individuals are better than others at maximising resource gain, or that NDVI, my proxy for available resources, does not fully capture what is important for

individuals. There are a number of reasons why this might be the case. First, there can be other sources of seasonal resources, such as anthropogenic resources (e.g. bird feeders in gardens, Job and Bednekoff 2011); some of these sources might be at a scale that is missed by my hexagonal grid.

Second, NDVI data was not available for the whole time period covered by the ringing dataset (see Fig. C2). Note that for this reason, temperature data was also considered as an aggregate for the season, regardless of the year of the ringing data (Worldclim database: average for the years 1970-2000, see Methods section). As I will discuss it in Chap. 7 (section 7.3.2.1), this temporal mismatch can be problematic as migratory patterns have been found in several species to have changed through time – mostly in response to changing climate (Adriaensen, et al. 1993, Berthold 1999, Fiedler 2003, Parmesan and Yohe 2003).

Additionally, I could not account for competition in this study, even though it is likely to have a strong effect on the amount of resources available. Indeed, there can be a high surplus in resources from one season to the next at a certain location, but if there are many birds breeding or wintering there, the amount of resources available to each individual will be limited.

Besides, because I do not take inter-annual variations into account (the only temporal component of this study is the season), some patterns due to year-to-year variation in resources might not be captured. For instance, resource blooms in certain years have been proposed as an explanation for the irruptive migrations of Evening grosbeaks (Bock and Lepthien 1976). Such irruptions happen in several bird species, allowing them to track irregularly fluctuating resources (e.g. boreal finches tracking peaks of tree-seed and fruit crops productivity, owls tracking cycling rodent populations, or waterbirds tracking ephemeral wetlands; Newton 2008).

Finally, there might be within-season mobility, with individuals tracking resources that change even within the wintering season. For example, long-distance migrants like the Common cuckoo *Cuculus canorus*, the Red-backed shrike *Lanius collurio* and the Common nightingale *Luscinia megarhynchos*, are itinerant in Africa during the winter, tracking regional variations vegetation greenness during this season (Thorup et al. 2017).

More broadly, drivers of migration might be different in different seasons. For example, Dalby et al. (2014) found that the latitudinal distribution of waterfowl species was driven primarily by variability in plant productivity in the breeding season, but by potential evapotranspiration (a proxy for ambient energy, related with solar radiation) in the non-breeding season. Similarly, Somveille et al. (2015) found that the distribution of migratory birds' species richness is mainly

driven by minimum temperature in winter, but by resources in summer. Here I found that migrating allows individuals to better track their thermal niche than staying at the winter location year-round, but also to much better track it than staying at the summer location year-round (Figure 5.1), suggesting that the benefits in terms of temperature range are more important for the choice of the winter location.

5.5.3. How do individuals perform along this trade-off? (Question 3)

Given the existence of a trade-off between migratory distance (reflecting the cost of the migratory journey) and benefits in terms of thermal niche tracking and resources, I then investigated how this trade-off is optimised (which costs and benefits are prioritised by individuals). When comparing observed individual strategies with alternatives, my results indicate that the costs of migratory distance is the most important factor (Figure 5.5), with individuals selecting for consistently shorter-than-available migratory distances.

Even though detectable at both within-range and continental scales, this effect is much weaker within the range; this result is consistent with the absence of latitudinal structure in how individuals redistribute within the species range from one season to the next, as found for most species in the previous chapter. It is also not surprising that the effect at the continental scale would be stronger, as the wider scale allows for a much larger range of options in terms of migratory distance.

The only species not showing a preference for short distances within the range is the Evening grosbeak, for which strategies ranked around average (Figure 5.5), consistent with the irruptive migratory pattern mentioned above, and with my finding in the previous chapter that individuals from this species randomly mix along the latitudinal axis from one season to the next.

In contrast, when compared with alternatives, individual strategies do not perform any better than the median strategy, based on thermal niche tracking and resource availability (around the median strategy within the range, and even worse than the median strategy at the continental scale; Figure 5.5). Although individuals track better their thermal niche than if they did not migrate (at the individual level, Figure 5.1; at the species level, Somveille 2015, Chap. 4), there is no perfect thermal niche tracking (at the individual level, Figure 5.5; at the species level, Boucher-Lalonde et al. 2014; Laube et al. 2015). This suggests the existence of additional constrains, preventing individuals from doing as well as they could along these axes, or simply

a decreasing marginal benefit of going to increasingly resource-rich areas, or of increasingly tracking their thermal niche, that does not balance the cost of migrating increasingly far.

The difference between my results and other results at the species level (Somveille (2015, Chap. 4) found that species perform better than alternatives in terms of both thermal distance and resource scarcity) may be explained by various differences between their analyses and mine. First, here I constrain alternative options 1) to be within either the range or North America, instead of considering the whole Western Hemisphere, and 2) to be made of a winter location south of the summer location, therefore reducing the number of poorly performing alternatives. Second, the species in my study differ from the ones in Somveille (2015, Chap. 4): I analysed only species whose winter and summer ranges highly overlap, whereas Somveille (2015, Chap. 4) only included species whose seasonal ranges do not overlap by more than 20%.

5.6. Conclusions

Overall, my results suggest that drivers that were found to play a role at the species levels are also important at the individual level, but their effect is weaker. This indicates the presence of more stochasticity in the redistribution of individuals within the species range than in the redistribution of species themselves. This is not surprising as underlying processes driving individuals' behaviour are expected to be more apparent when large aggregates of individuals are analysed together. Additionally, as the temperature range between an individual's locations is no smaller than the temperature range with any other location within the species' spatial range, this does not support the hypothesis of individual specialisation. I also found results suggesting that, for the species I analysed, when migratory strategies are compared with alternatives, minimising migratory distance plays a stronger role than encountering optimal environmental conditions.

Despite its limitations, the dataset I used here was the best I had access to to test these hypotheses, because it contains information on a large number of individual birds. In general, studying individuals can be a valuable complementary approach to species-level macro-ecological studies, as it allows to have information on within-species spatial patterns (e.g. where individuals tend to be migratory vs. resident, who is migrating where). Fortunately, with improvement in technology, and new projects, there will be scope for carrying out similar studies without some of the limitations of ringing data. Such projects include the ICARUS project - a large-scale fitting of birds with light GPS tags and other loggers, transmitting daily

data via satellite (https://icarusinitiative.org/) – and the Motus Wildlife Tracking System – a collaborative research network of radio telemetry stations tracking animals equipped with radio transmitters, spreading out from the Arctic to South America (https://motus.org/). In particular, since these new data have been all collected over the past few years, detailed climatic information would allow to take inter-annual variability into account. And as they provide more than two locations per individual, these data would also allow to correct for problems with the temporal definition of breeding vs. non-breeding seasons or with within-winter mobility (by only considering a location when the bird has settled, or considering multiple winter locations per individual). Additionally, there would also be a chance to get other types of information on the individuals tagged (e.g. sex) – information that was not available for enough individuals in my dataset. Finally, other sources of data would also allow to refine this study. For example, abundance maps produced by eBird (online species checklist program, http://ebird.org/) might provide ways to take competition into account and assess its importance for driving the choice of where to migrate.

5.7. Acknowledgements

I am grateful to all the volunteers who collected the banding data and to the many employees of the Bird Banding Lab who worked to curate the data. The data was also used for Chapters 5 and 6 of this thesis.

6. To migrate or not to migrate: do anthropogenic effects buffer the costs and benefits of migration at the individual level?

6.1. Abstract

Migratory birds move seasonally between two ranges. Some species are partially migratory, i.e. some individuals migrate and some remain residents. Previous studies have found that migrating allows individuals/species to track better their niche and secure an increased access to resources than if they had remained residents. Migration can thus be seen as a way to escape unfavourable conditions. Additionally, anthropogenic factors can influence how favourable conditions are for birds, with urban areas buffering against seasonal environmental variability. Do any of these factors (climate, resources, presence of humans) influence the migratory behaviour of individuals? Here, I test the influence of winter temperature, summer resource surplus, as well as human population density on the probability of individuals to remain resident. For this I use a ringing/recovery dataset on nine species of migratory North American passerines and near passerines, providing information on where each individual spent the winter and the summer and test the influence of anthropogenic and non-anthropogenic environmental conditions on the probability of individuals to stay as a resident. I find that more favourable conditions (milder winter temperature, higher summer resource surplus and, for some species, higher population density) increase the probability to stay. As global change is affecting these conditions, individual migratory strategies could be impacted in the future.

6.2. Introduction

Migration is the seasonal redistribution of individuals between two ranges. It has been suggested to allow species – and, to a certain extent, individuals – to better track their climatic niche throughout the year, as well as to increase their access to resources (at the species level, Somveille et al. 2015; at the individual level, Chapter 5, this thesis). However, migration also has costs. Indeed, the journey can be highly energy-demanding (Wikelski et al. 2003) and comes with several associated mortality risks (e.g. weather-induced mortality risks, collisions with infrastructure; Newton 2008), as well as potential difficulties in finding a free territory when after the spring migration (Kokko 2011).

Many studies have been made on the consequences of such costs and benefits (e.g. how the environmental influences the distribution of migratory species; Hurlbert and Haskell 2003, Somveille et al. 2015). These studies were mainly done at the species level, but ultimately individuals are the ones making the decisions of whether or not to migrate. Focusing on individuals is especially important as in some species, different individuals make different decisions regarding the balance of the above-mentioned costs and benefits. Indeed, 'partial migration' happens when some individuals migrate and some do not, and is common for bird species. For example, in a review of Austrian landbirds, Chan (2001) found that 44% of 155 non-passerine species and 32% of 317 passerines studied were partial migrants.

Migratory behaviours can potentially be very flexible, as demonstrated by some recent changes, with populations switching from migratory to sedentary (see Newton 2008 for a review). For example, British and mid-European populations of Eurasian blackbirds *Turdus merula* became mainly resident (Berthold 1993, Main 2000) and Great crested grebes *Podiceps cristatus* in the Netherlands became resident in increasing proportions (Adriaensen, et al. 1993). Less frequently, populations have switched from sedentary to migratory. For example, European serins *Serinus serinus* became migratory when spreading north in Europe (Berthold 1999). Other populations have changed – shortened, mostly – their migratory routes. In particular, several European migrants that wintered in Africa south of the Sahara now overwinter in higher numbers in Southern Europe (e.g. white storks *Ciconia ciconia*, Gilbert et al. 2016).

Many of these changes are likely to reflect global change, altering the balance between the costs of being resident (being exposed to harsh winter weather, having access to a low amount of resources and facing potentially high levels of competition) and the costs of migrating (energetic costs and mortality risks), in turn affecting migratory behaviours. Some areas get

waters that now remain open where they used to freeze in winter) but can also potentially make some other areas too dry for birds to breed.

Global change also comes with changes in land use, for instance with the conversion of natural habitat into agricultural lands or urban areas. Urban areas are traditionally seen as detrimental for most birds, with species richness usually decreasing with increasing urbanisation (Clergeau et al. 1998, Lee et al. 2004). However, although mostly because of a few dominant species, total abundances can be positively affected by urbanisation (Jokimäki et al. 1996, and, up to a certain level, Tratalos et al. 2007). This is likely to be because urban areas can provide nesting opportunities (e.g. species that nest on buildings, like European starlings *Sturnus vulgaris*, House sparrows *Passer domesticus*, or Chimney swifts *Chaetura pelagica*, Alsop 2002) and additional resources (e.g. bird feeders, landfills, etc.). Beside positive effects on egg laying, or adult and juvenile survival (Robb et al. 2008), supplementary feeding has also been found to affect species ranges (e.g. bird feeders predict even better than winter temperature the northern limit of the range of the non-migratory Carolina wren Thryothorus ludovicianus, Job and Bednekoff 2011) and even migratory routes (e.g. Blackcaps *Sylvia atricapilla* breeding in Germany now wintering in Britain instead of Spain because of climate change and supplementary feeding, Plummer et al. 2015).

Urban areas also tend to be warmer than surrounding non-urban areas, an effect called the 'heat island' effect, which can potentially protect birds from the harshness of winter (Shochat et al. 2006). Finally, artificial lights in urban areas can potentially increase the available time for foraging per day (although Ockendon et al. 2009 did not find evidence for an effect of urban vs. rural areas on how early in the morning birds start foraging).

Overall, given that urban areas tend to buffer against the temporal variability in environmental conditions (Shochat et al. 2006), being in an urban area is likely to reduce the costs of being resident (through milder winter temperatures and more abundant year-round resources). Therefore, the probability to remain as resident should be higher (1) in winter, in areas where winter temperatures are high and/or in more urbanised areas, and (2) in summer, in areas where non-anthropogenic resources are abundant and/or in more urbanised areas. Here I use a large-scale ringing dataset (USGS Bird Banding Laboratory, 2016) providing individual information on migratory status for nine North American passerine and near passerine species, to test the effects of winter temperature, summer non-anthropogenic resource surplus and level of urbanisation (using human population density as a proxy) on the probability to remain as residents.

6.3. Methods

6.3.1. Individual data

I used individual breeding and non-breeding locations from the North American ringing/recovery scheme (USGS Bird Banding Laboratory, 2016). Non-breeding locations were defined as observations of alive birds happening between December and February, and breeding locations as observations of alive birds between June and August. Only individuals for which I had at least one breeding and one non-breeding location were kept. In cases where several observations were made for the same bird in a season, I always kept the first. Based on the distribution of distances between the breeding and the non-breeding records, resident birds were defined as individuals recovered less than 50km away from their ringing location during the opposite season, whereas migrant birds were those that had moved more than 50km between the breeding and the non-breeding seasons.

I focused on nine species for which reasonable amounts of data were available: the American goldfinch (*Spinus tristis*), the American robin (*Turdus migratorius*), the Brown-headed cowbird (*Molothrus ater*), the Common grackle (*Quiscalus quiscula*), the European starling (*Sturnus vulgaris*), the Evening grosbeak (*Coccothraustes vespertinus*), the House finch (*Haemorhous mexicanus*), the Purple finch (*Haemorhous purpureus*), and the Red-winged blackbird (*Agelaius phoeniceus*). See Chapter 4 for a more detailed description of each species.

The Eastern House Finch population has likely been introduced from the isolated Western population, where individuals are mostly sedentary (Able and Belthoff 1998). In its most recent range, it is a partial migrant. In order to focus only on the part of the range where there are both resident and migratory individuals, I excluded the Western population from the analysis by selecting only sightings occurring east of 95°W.

6.3.2. Environmental data and human population density

6.3.2.1. Winter temperature

To measure winter temperature, I used monthly means from the Worldclim database (average for the years 1970-2000, resolution 30'', Hijmans et al. 2005) for the months of December to February, which I further aggregated to a winter mean. For each individual, I extracted the winter temperature at its summer location (see the extracted data for migrants vs. residents in Figure C1).

6.3.2.2. Summer resource surplus

As an indicator of resources (food, nesting sites and roosting sites), I used the Normalized Difference Vegetation Index (as in Hurlbert and Haskell 2003, Somveille et al. 2015, and Chapter 5 in this thesis). I used monthly means from NASA's Earth Observatory (resolution 0.1˚; available from https://neo.sci.gsfc.nasa.gov/). As in Chapter 5, to avoid focusing on an unrepresentative year, and because there was no available data old enough to cover the whole period of my ringing data, I created means over 2006-2015, and then created a winter mean using the months of December to February. From these I calculated the summer energetic surplus at each individual's winter location as $NDVI_{summer} - NDVI_{winter}$ (see Fig. C1 for the extracted data).

6.3.2.3. Human population density

I considered human population density as a proxy for the level of urbanisation. The median ringing/re-sighting year for the pooled species data was 1956 (interquartile: 1946-1968, see Fig. C2 for the detailed distributions). The publicly available reconstructed map of global population density that is closest to this date is from 1970, available from SEDAC (http://sedac.ciesin.columbia.edu/data/set/popdynamics-global-pop-density-time-series-estimates/metadata).

I extracted the mean population density in a buffer of 5km around each individual location, and log transformed it using log(x+1). This transformation improved the distribution of this variable which spans several order of magnitude. It also allowed me to take into account the fact that the effect of increasing the human population density is likely to be stronger in areas that are sparsely populated than in areas that are already densely populated (see the data for migrants vs. residents in Figure C1).

6.3.3. Analyses

First, the results in Somveille (2015, Chap. 4) indicate that the location of species non-breeding distributions reflects a tendency to avoid harsh winter temperatures. If winter temperature is an important constraint to residency in the winter also at the individual level, I expect that the lower the winter temperature, the less likely for individuals to remain as residents over winter.

Second, migration has also been suggested to allow species to have a better access to resources (Somveille, 2015, Chap. 4). In the previous chapter of this thesis, I found similar results at the individual level for the species under study here. Resources are more likely to be important during the breeding season, because of the extra energetic cost of reproduction. If resources are

indeed an important constraint to residency in summer at the individual level, I expect that the higher the resources in summer, the more likely for individuals to remain as residents over summer.

Last, urban areas are likely to buffer against low temperatures in winter and low resources in summer. If it is the case, I expect, individuals to be more likely to be residents in more densely populated areas (my proxy for urbanisation), in both seasons.

To test these three predictions, I split my dataset into summer locations and winter locations. For the summer locations, I fitted a binomial Generalised Linear Model (logit link), with the resident (1) vs. migrant (0) status of each bird as a response, and log(human population density + 1) and the winter temperature at each location as explanatory variables. For the winter locations, I repeated the same analysis but using the summer resources surplus instead of the winter temperature. Note that I did not model the probability of birds to be present at each location, but rather their probability to remain at that location, given that they were present in the other season.

I standardised variables prior to modelling to allow for the comparison of estimated coefficients (i.e. β coefficients), using the following formula: (x – mean(x))/sd(x). To select the best model, I used a backwards stepwise selection procedure using AIC. To correct for multiple testing, I used a sequential Bonferroni correction. All analyses were done in R (R Core Team 2017).

6.4. Results

6.4.1. Staying at the winter location over summer

For most species, the probability of staying as resident at the winter location was positively related with the amount of resources (NDVI surplus) in that location during summer (American goldfinch, Brown-headed cowbird, European starling, House finch and Purple finch;

Table 6.**1**, Figure 6.1). This supports the hypothesis that the availability of resources during the breeding season affects the migratory decisions of individuals. Additionally, for most species, the probability to be resident was significantly higher in more densely populated areas, consistent with the hypothesis of a buffering effect of human population density on low summer non-anthropogenic resource availability. This was the case for the American robin, the Common grackle, the European starling, the House finch and the Purple finch (Table 6.1, Figure 6.1). The effect of these two variables (summer NDVI surplus and human population density) on the probability to remain as a resident was never significantly negative.

6.4.2. Staying at the summer location over winter

For all species, the warmer the winter temperature, the higher the probability to be resident, although this effect was only significant for the American robin, the Common grackle, the House finch and the Red-winged blackbird (Table 6.2, Figure 6.1). This is supporting the hypothesis that winter temperature acts as a constraint to winter residency. The effect of human population density at the summer location was only significant for the European starling and the Purple finch, and was positive in both cases (Table 6.2, Figure 6.1), consistent, for these species, with the hypothesis that human population density acts as a buffer on low winter temperature.

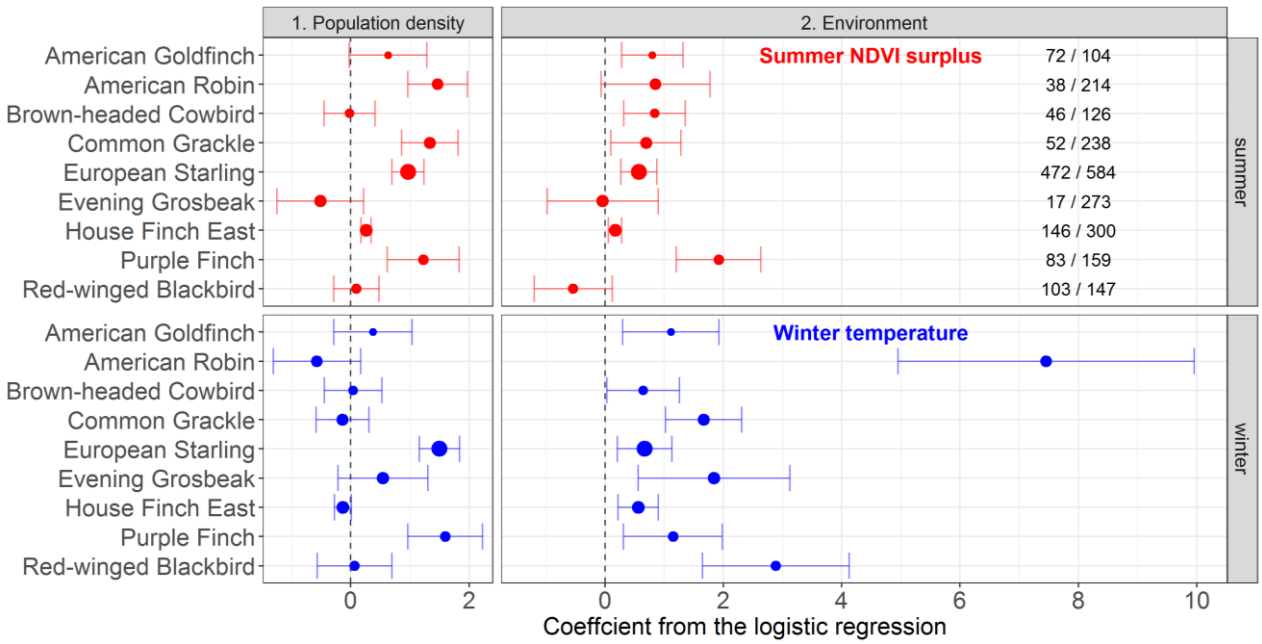

Figure 6.1: Estimated coefficients of the binomial GLMs for each species *with 95%*

confidence intervals. The size of the points represents the sample size, and the ratios in the top-right panel present the ratio of residents over the total sample size.

Table 6.1: Estimated coefficients and p-values for the two variables in the binomial GLMs *(human population density and summer NDVI surplus), with staying at the winter location in the summer (1) vs. migrating (0) as the response variable. P-values are in bold when the effect is significant after a sequential Bonferroni correction.*

	Species	Population coefficient	Population p-value	NDVI coefficient	NDVI p-value
1	American Goldfinch	0.63	6.03e-02	0.80	**2.58e-03**
2	American Robin	1.47	**1.25e-08**	0.86	6.93e-02
3	Brown-headed Cowbird	-0.02	9.33e-01	0.84	**1.49e-03**
4	Common Grackle	1.34	**4.37e-08**	0.69	2.16e-02
5	European Starling	0.97	**2.47e-12**	0.57	**2.10e-04**
6	Evening Grosbeak	-0.51	1.68e-01	-0.04	9.34e-01
10	House Finch East	0.26	**4.55e-09**	0.17	**3.12e-03**
8	Purple Finch	1.23	**7.93e-05**	1.92	**1.30e-07**
9	Red-winged Blackbird	0.10	6.28e-01	-0.54	1.10e-01

Table 6.2: Estimated coefficients and p-values for the two variables in the binomial GLMs *(human population density and winter temperature), with staying at the summer location in the winter (1) vs. migrating (0) as the response variable. P-values are in bold when the effect is significant after a sequential Bonferroni correction.*

	Species	Population coefficient	Population p-value	Temperature coefficient	Temperature p-value
1	American Goldfinch	0.37	2.68e-01	1.11	**7.19e-03**
2	American Robin	-0.57	1.30e-01	7.46	**5.28e-09**
3	Brown-headed Cowbird	0.04	8.69e-01	0.65	**3.85e-02**
4	Common Grackle	-0.14	5.39e-01	1.67	**3.95e-07**
5	European Starling	1.50	**3.19e-18**	0.67	**4.45e-03**
6	Evening Grosbeak	0.55	1.60e-01	1.84	**4.87e-03**
10	House Finch East	-0.14	6.45e-02	0.56	**1.35e-03**
8	Purple Finch	1.59	**7.90e-07**	1.15	**7.06e-03**
9	Red-winged Blackbird	0.07	8.38e-01	2.89	**4.96e-06**

6.5. Discussion

6.5.1. Summary

Here I investigated what drives the choice of individuals to remain resident in nine partially migratory North American bird species, using a large scale ringing dataset (USGS Bird Banding Laboratory, 2016). I found that for most species, individuals are more likely to stay from one season to the next if the environmental conditions in the next season are more favourable (warmer winter temperature or higher summer resource surplus). Additionally, I found that for some species, human population density also has an effect, with birds more likely to be resident in more densely populated areas.

6.5.2. Environmental effects

The effects of non-anthropogenic resources and winter temperature are consistent with previous findings both at the species and at the individual level focusing on migrants. Indeed, migrants have be found to experience more favourable conditions than if they stayed at the same location all-year-round; at the species level, Somveille 2015; at the individual level, Chapter 5 in this thesis). Here I extend those findings with results indicating that individuals are more likely to stay resident in areas for which the costs of staying is limited, i.e. could not be reduced much by migrating.

6.5.3. Human population density

The effect of human population density is more variable. Indeed, although human population density increases the chances of individual birds to stay at their winter location over summer for several species (American robin, Common grackle, European starling and Purple finch), the European starling and the Purple finch are the only two species for which human population density increases the chances of individuals to stay at their summer location over winter (Figure 6.1).

For some species, I found no effect of human population density on the probability to stay as a resident, regardless of the season (American goldfinch, Brown-headed cowbird, Red-winged blackbird). This could be in part due to limited statistical power, as these species have the smallest number of records (respectively 104, 126 and 147).

It is also possible that, for these species, the effect of population density is not linear – or not even monotonic. Indeed, densely populated areas can be associated with lower bird densities (e.g. in Taiwan, Lee et al. 2004), but for intermediate levels of urbanisation, managed green spaces are often more productive than the surrounding wildlands (Imhoff et al. 2000), leading

to humped-shaped relationships between species richness, or abundances, and levels of urbanization (e.g. Tratalos et al. 2007). Additionally, humans can also have effects that are unrelated to their density: for example, humans can provide resources through agriculture (Foley et al. 2011), but in these areas, human population densities are relatively low.

Despite these possible limitations, the absence of an effect of population density for some species can also be related with how much humans can make the habitat more favourable to these species, i.e. how favourable the "natural" habitat is in the first place, as well as how dependent these species are on anthropogenic resources and infrastructures. However, it is hard to predict for which species human population density will increase the probability that individuals will remain resident. For example, whilst I might not have expected any effect for Red-winged blackbirds, which live in marshes and agricultural fields and do not feed on anthropogenic sources of food (Alsop 2002), an effect could have been predicted for American goldfinches which are common in suburbs, parks and backyards, and tend to visit garden feeders (Alsop 2002). However, I found no effect of population density on the migratory decisions for either of these two species. Similarly, both European starlings and House finches are known to be highly associated with cities and they both are more likely to remain resident in winter when found in cities, but at their summer location, the effect is only present for the European starling.

Overall, there is a more prevalent effect of human population density on individuals' strategies in the summer than in the winter (Figure 6.1). This can be due to the fact that below a certain winter temperature, the energetic cost of staying might be so high that, regardless of human population density, individuals have to leave (as they get below a critical isotherm corresponding to a bottom limit on birds' metabolic rate, Root 1988). This interpretation is also consistent with the fact that, overall, winter temperature tends to be the variable that has the strongest effects on the probability of staying at the summer location.

6.5.4. Potential caveats

There are potential limitations concerning the dataset used and the tests performed, which I will present below. However, most of these limitations should, if anything, make the test more conservative, so I can be confident about the effects that I detect (

Table **6.1** and Table 6.2).

First, partial migration could emerge from a mix of consistently migrating and consistently staying individuals (e.g. Gillis et al. 2008), potentially emerging from intrinsic differences between migrants and residents regarding the various costs (e.g. basal metabolic rates and cost of thermoregulation, Nilsson et al. 2011) or from individuals whose strategies change over time, possibly in response to changing environmental conditions (e.g. Shaw and Levin 2011). As it only contains one pair of locations for each individual, my dataset does not allow to distinguish these two scenarios, so individuals considered as migrants actually could potentially be residents some years (and the conversely). Under the first scenario, the probability of individuals migrating would not be necessarily due to where they are, but also possibly to who they are (e.g. due to their dominance status, Ketterson and Nolan 1979; or body size, Belthoff and Gauthreaux 1991). Under the second scenario, limitations may arise from the fact that I cannot take year-to-year variability into account. However, in both cases, these limitations are likely to make the tests more conservative.

Second, records in the Bird Banding Laboratory data are spatially clustered, and might be more likely to occur in places where there are more people (hence more people to ring birds and to record the presence of ringed birds), but also potentially in places where people are more nature-friendly, and hence more inclined to ring/record sightings (see discussion about spatial bias in Chapter 4). However, this spatial clustering is unlikely to affect migrants and residents differently, so for a given place, the probability to be resident should not be affected by a potential spatial bias in recordings.

Third, there can be issues arising from the temporal mismatch between my ringing data (see Fig. C2 for a distribution of records through time) and my explanatory variables (e.g. temperature averaged over 1970-2000, population density in 1970). This issue will also be discussed in section 7.3.2.1. However, if anything, I would expect this potential mismatches to make the signal of the drivers of migration vs. residency less clear.

6.5.5. Implications

The effects found here are likely to influence the response of species to climate change. First, as individuals of the studied species were more likely to be resident in areas where winter temperature was milder, an increase in temperature in these areas could potentially lead to an increase in the proportion of residents in the summer ground (providing that the habitat remains intact). Additionally, although the effects of human population density on the tendency to be

resident might change in counter-intuitive ways (due to potentially non-linear effects), and although species might need time to adapt to new conditions, human population is increasing overall and becoming more urban, which might make these birds more likely to adopt resident strategies.

7. General discussion

7.1. Introduction

In this thesis I argued that information on individual movement can help understand how species-level patterns of space use emerge from individual decisions. I first presented a review of existing methods used to quantify individual differences in geographical, behavioural or environmental preferences. I then developed a method for quantifying such differences based on individual tracking data, and applied this method to two species of albatrosses, and found that although I could detect geographic differences (foraging site fidelity), signals for environmental differences (individual specialisation) were weaker.

In the following chapter, I studied the latitudinal redistribution of individuals within the breeding and non-breeding ranges of nine migratory passerines and near passerines and found that for most species, this redistribution patterns are indistinguishable from random. I went on investigating the drivers of individual migratory decisions and my results suggested that although individuals track better their climatic niche and seasonal surpluses in resources by migrating than they would by staying, there are trade-offs between these benefits of migration and the cost of migratory distance, and, considering all options available, most individuals in these species favour short-distance migration. Finally, I tested the effect of the environment on the decision to migrate vs. remain resident and found that the more favourable the conditions (warmer winter temperature and higher seasonal surplus in resources – but also the buffering effect of urban areas), the more likely individuals are to remain resident.

In this final chapter, I will first discuss issues related with the detection of individual differences in space use (appropriate data and methods, existing patterns, limitations and perspectives). Then I will comment on the potential drivers of such individual differences (individual differences in environmental preferences, individual choices along a trade-off) as well as limitations and perspectives. I will then end with a discussion of the general implications of such differences and of what drives them.

7.2. Are there individual differences?

7.2.1. State-of-the-art and contribution of this thesis

7.2.1.1. Methods of detection

In order to identify and quantify intraspecific differences in space use, individual movement data are required. Several types of data have been used to study these differences at various scales. Ringing data have been used to understand levels of connectivity between breeding and non-breeding ranges (how populations redistribute within species ranges, e.g. Ambrosini et al. 2009, Finch et al. 2017, Procházka et al. 2017). If ringing data have the advantage of allowing large scale studies, tracking data – due to the many locations they provide per individual – allow the study of *consistent* individual differences (i.e., in geographical space, 'route fidelity', e.g. Dias et al. 2013; and 'site fidelity', e.g. Wakefield et al. 2015, Patrick and Weimerskirch 2017).

In the above-mentioned situation when multiple measurements per individual are available (as it is the case with tracking data), it is possible to estimate the degree of consistency in the preferences of individuals, given that the appropriate statistical methods are used. Although this section (section 7.2) focuses primarily on geographical space use, these considerations also apply to environmental space use. I reviewed the large variety of existing methods to statistically detect consistent individual differences in space use and preferences. Most of the recent methods developed include the use of mixed models, where individual ID is fitted as a random effect, and individual- and population-level variance components are used to calculate repeatability measures.

However, all mixed models are focused on one dimension at a time. Multiple environmental variables can be taken into account in the same mixed model with the use of random slopes but, in such a framework, each variable still has to be considered separately. However, there can be interactions between environmental variables, justifying the use of a multidimensional approach. In this thesis, I presented a new method for identifying consistent individual differences in both geographical and environmental space use. Note that although I developed it mainly for applications in environmental space (to take into account the multi-dimensionality of the niche), this method also allows calculating within- and between-individual overlaps of use in geographical space.

7.2.1.2. Existing patterns

Once the correct data are collected, and the appropriate statistical methods are used, intraspecific differences in space use can be identified. In this thesis, for example, for the nine species of (near) passerines under study in Chapters 4 to 6, I found that the latitudinal redistribution of individuals between the breeding and the non-breeding season is mostly indistinguishable from random (i.e. for most species, it does not seem to follow the textbook patterns suggested by Newton (2008) of chain vs. leapfrog migration). However, longitudinally, there seems to be some structure: individuals breeding further east of the range tend to also winter further east, and conversely, suggesting some degree of migratory connectivity (*sensu* Webster et al. 2002). The studies that have estimated migratory connectivity so far suggest that migratory connectivity can be highly variable between species. For example, in Barn swallows *Hirundo rustica*, connectivity is high and associated with migratory flyways (Ambrosini et al. 2009); whereas in several long-distance migrants, overall migratory connectivity is low, i.e. there is a high degree of inter-population mixing between the breeding and non-breeding ranges (Korner-Nievergelt et al. 2010 on Common nightingale *Luscina megarynchos*, Trierweiler et al. 2013 on Montagu's harrier *Circus pygargus*, Finch et al. 2017 on 98 populations of 45 species). See Chapter 4 for a more thorough discussion of these results.

I also provide additional evidence for the nine species I have focused on for the existence of different strategies regarding whether to migrate or not (i.e. partial migration), but also for the wide within-species variability in distances migrated. This finding is in line with mounting evidence for partial migration in a wide range of taxa (Chan 2001, for example, found that 44% of the non-passerine and 32% of passerines from Australia that they reviewed were partial migrants). My results also echo results on differential migration (e.g. Durell 2000 for shorebirds), although here I did not relate such variability in migratory distances to factors such as age or sex.

Last, although the ringing data I use in Chapters 4 to 6 did not allow the study of the *consistency* of individual spatial patterns (as I have information on only one choice per individual), the other data set used in this thesis – tracking data for two albatross species – allowed me to study these aspects. Doing so, I identified consistent individual differences in space use (i.e. site fidelity) for both species under study (Chapter 3).

7.2.2. Limitations and perspectives

7.2.2.1. Sample sizes

A first issue when trying to detect individual differences is sample size, and particularly so when trying to detect *consistent* individual differences. Although in this section (section 7.2), I focus mostly on geographic patterns, the issue of sample size arises in all cases when I try to estimate individual consistency (including in resource or habitat preferences).

There is little literature on the appropriate number of individuals or of measurements per individual that are needed to detect consistent individual differences: the only recommendations I could find were in Wolak et al. (2012), who provided a formula to estimate the combinations of {number of individuals, number of measurements per individual} that allow obtaining a certain confidence interval. However, this formula is only relevant in the specific context of repeatability estimates from ANOVAs and not straightforward to extend to multidimensional scenarios (see Chapter 2 for details). In particular, in a framework like the one I developed in Chapter 3 – using hypervolumes of (geographical or environmental) space – no such formula can be defined. A promising approach to estimate the necessary sample sizes would be to carry out simulations and estimate the sensitivity of the Individual Specialisation Index (*ISI*) results on these sample sizes. An approach like the one in (Clay et al. *in prep*) can potentially be used, rarefying the data and checking when (and whether) the *ISI* values start plateauing (however, such an approach requires a sufficiently large dataset to rarefy).

In any case, there is always a risk not to sample representative individuals, or to miss those individuals that behave differently. For example, for seabirds, breeders are the most tracked category because they are easier to catch, but it is possible that juveniles, immatures or failed breeders behave differently (having different space use and different resource requirements, see Phillips et al. 2017 for a review). Should we therefore sample individuals of as many categories as possible? This would allow drawing conclusions that are more general – and therefore more useful for making predictions of conservation value. However, if resources are limited, this would come at the cost of reducing the sample size per category, adding some unexplained sources of variation.

As datasets become larger, thanks to the availability of more accurate, higher resolution and cheaper and lighter loggers (Ponchon et al. 2013), we have increasing power to control for factors that may bias the results. Additionally, information such as age or sex are more commonly recorded, and loggers are being developed that do not require the recapture of

individuals, hence allowing the study of broader categories of individuals (e.g. including failed breeders).

7.2.2.2. Additional factors

As mentioned above, when studying individual differences, there can be multiple levels or sources of variation. Small numbers of sampled individuals (Chapter 3) and lack of information on enough of them (Chapters 4 to 6) prevented me from investigating these effects, but individual differences can sometimes be attributed to known intrinsic factors, such as age or sex. For example, sexual segregation in foraging areas have been found in seabirds (e.g. in albatrosses *Thalassarche melanophrys* and *T. Chrysostoma*, Phillips et al. 2004b). Sexual differences have also been found in migratory behaviours (e.g. differential migration according to sex, e.g. in chiffchaffs, *Phylloscopus collybita* and *P. ibericus*, Catry et al. 2005). Age differences have been found in birds in terms of foraging behaviour (e.g. sanderlings *Calidris alba* and northern gannets *Morus bassanus* increase site fidelity with age; Lourenço et al. 2016, Votier et al. 2017), but also in how far and where individuals migrate (e.g. Durell 2000 for a review on differential migration in shorebirds). Finally, breeding status has also been found to influence spatial foraging behaviour (see Phillips et al. 2017 for a review).

These sources of variation can be important to consider when trying to understand the response of populations to various threats. For example, if males and females forage in different areas (e.g. Phillips et al. 2004b), and one of these areas is particularly affected by anthropogenic threats, this can affect sex ratios and therefore reproduction (see Phillips et al. 2017). Similarly, if adults vs. juveniles (or successful vs. failed breeders) are affected differently, the consequences will not be the same. This is particularly true if the individuals that are more exposed to the threats are the ones that make the biggest contribution to the population growth rate (individuals of 'high parental quality', Moreno 2003).

7.2.2.3. Spatial and temporal scales

If there are (consistent) individual differences, it is pertinent to wonder at which spatial and temporal scale they emerge. For example, the emergence and detectability of site fidelity is likely to be scale-dependent, as: (1) at some spatial scales, the whole species might use the same area, but at finer spatial scales, individuals might differ; but conversely, (2) if foraging strategies are hierarchical (i.e. predators first travelling to large-scale patches, then looking for prey within these patches, Fauchald et al. 2000), individual foraging site fidelity might decline below the coarse scale, as individuals might change their foraging areas within familiar large-scale

patches (e.g. northern gannets *Morus bassanus* are more consistent in the directional arc they follow when leaving the colony than to exact foraging areas, Wakefield et al. 2015).

From a temporal perspective, individuals can appear to be site faithful (and potentially specialised) at short time scales but eventually use wider areas over longer periods of time. The flexibility (or not) in these individual differences in space use has conservation implications regarding the ability for individuals or species to recover from the destruction of the habitats in certain areas or from geographically recurrent threats (see section 7.4). Additionally, the duration of site fidelity can provide insights into its drivers (e.g. win-stay/lose-shift strategy, site familiarity, environmental preferences, see Wakefield et al. 2015 for details). The next section of this discussion (section 7.3) will focus only on those drivers that are related to environmental conditions.

7.3. Drivers of individual differences

7.3.1. State-of-the art and contribution of this thesis

7.3.1.1. General state-of-the-art

Several studies have investigated the drivers of species distributions (see the abundant Species Distribution Models literature, Elith and Leathwick 2009). Some have also investigated the drivers of movement at the species level, mostly in the context of bird migration (e.g. Somveille 2015, Chap. 4), including biotic and abiotic environmental conditions (e.g. winter harshness or resource abundance) and accessibility. However, these studies do not inform us on what happens within a species range.

At the individual level, individual tracking data have been providing better and better information on what drives individual movement (e.g. using Resource Selection Functions, Manly et al. 2002). However, taking into account intraspecific in models is recent and rare (e.g. Hebblewhite and Merrill 2008) and it is even more infrequent to go beyond correcting for this variability and actually focus on and try to understand it (but see Wakefield et al. 2015, and Courbin et al. *in prep*).

In this thesis, I focus on two potential drivers of intraspecific variation in space use: (1) individual environmental preferences (that can only be tested for using repeated measurements per individual, see Chapters 2 and 3) and (2) different individual decisions along a trade-off (that can be addressed using ringing data, see Chapters 4 to 6).

7.3.1.2. Individual preferences

Even though I detected a statistically significant signal of individual specialisation (Chapter 3), it is hard to understand whether or not such individual specialisation is creating individual differences in space use. Wakefield et al. (2015) discuss three hypothesis about what can drive individual foraging site fidelity (IFSF) in northern gannets *Morus bassanus*: a win-stay/lose-shift strategy, individual specialisation and site familiarity. They do not find support for the first two hypotheses, which leads them to raise the third hypothesis, for which they cannot properly test. In particular, they found a correlation between IFSF and individual specialisation (here in terms of relative sea surface temperature, a proxy for stratification regimes) within years but not between years. Patrick and Weimerskirch (2017) found similar results for Black-browed albatrosses *Thalassarche melanophrys*, with the environment characterised in terms of bathymetry. These results indicate that if there is a relationship between IFSF and individual specialisation, its temporal persistence is limited.

In Chapter 3, I found evidence for individual environmental preferences, but I cannot know if there is a causal relationship between these and geographical patterns. However, the fact that in some cases there is site fidelity without individual environmental specialisation similarly suggests that the relationship between the two is not that strong – and that in this case, site fidelity could be driven by other mechanisms, such as site familiarity.

7.3.1.3. Trade-offs

Even if all individuals of the species have the same preferences for certain resources and environmental conditions, there might be trade-offs between satisfying these preferences and minimising other costs, and individuals might be making different decisions along that trade-off. This is what my results in Chapter 5 suggest, as the further individuals migrated, the better they tracked their niche and, to a certain extent, the higher they had access to seasonal resource surpluses. My results are consistent with results found at the species level (Somveille, 2015, Chap. 4; see discussion in Chapter 5 of this thesis).

My results also suggest that, along this trade-off, the favoured strategy (compared with available alternatives) is to reduce migratory distance, at the expense of climatic niche tracking and access to seasonal resource surpluses. In contrast, Somveille et al. (2015, Chap. 4) found that most species performed well in terms of these three cost and benefits when compared to alternative migratory strategies (see discussion in Chapter 5 of this thesis).

Somveille (2015, Chap. 5) found high predictive power of global migratory species' seasonal distributions in a mechanistic model balancing these costs and benefits. It would be interesting to explore if such predictions can be made at the individual level (e.g. predicting abundances).

Finally, along the trade-off between these costs and benefits of being in / going to each specific locations, individual choices may be driven by intrinsic individual differences. Indeed, there can be physiological differences between individuals (e.g. migrant vs. resident blue tits differing in their basal metabolic rate and the energetic cost of thermoregulation, Nilsson et al. 2011). Body size and dominance can also influence migratory decisions (Ketterson and Nolan 1979, Belthoff and Gauthreaux 1991).

7.3.2. Limitations and perspectives

7.3.2.1. Time resolution: potential mismatches between ecological processes and data

In this thesis, I could not always respect the coherence between the time scale of the relevant ecological processes and the time resolution of the data. For example, I only had one data point per season for the migratory passerines under study, whereas birds can sometimes move a lot within a season (mostly during the non-breeding season). There were also some temporal mismatches between the location data and the environmental data I could use (climate, NDVI and human population density data were not always available at the temporal resolution needed, or for the time period studied, see Chapters 5 and 6 in this thesis). Similarly, for the seabirds studied, it is also important for the scale of selection (and of the cues used by birds to select their habitat and where they go) to match the temporal scale of the environmental predictors (see Scales et al. 2016).

In Chapters 4 to 6, I might have created issues by treating as fixed a process that is actually dynamic. Indeed, by aggregating all ringing data – despite the fact that they belong to different time periods – I was not able to take into account the variation in migratory patterns that might have occurred during the overall study period. This can be problematic as both the migratory patterns and the drivers of migration have been found in several species to have changed through time: climate has changed and some species have shifted their ranges (Parmesan and Yohe 2003), migratory routes (e.g. Fiedler 2003) and even migratory strategies subsequently (e.g. migratory populations becoming increasingly resident, Adriaensen, et al. 1993, or the opposite, Berthold 1999).

In Chapters 4 to 6, I did not have enough data for each period to be able to split the analysis into different time periods and analyse the variation in migratory patterns. However, as more data becomes available, there should be scope for focusing on a restricted period of time (most probably a recent period), therefore removing the noise coming from potential fluctuations in time. Recent and more abundant data would also allow available environmental data to match the time scale of the individual movement data.

7.3.2.2. Properly quantifying costs and benefits

7.3.2.2.1 Which part of the spatial patterns depends on availability/accessibility vs. only preferences?

The distribution of individuals and their movement are also influenced by the accessibility of areas. In Chapters 4 to 6, I considered distance as exercising a cost on accessibility (and calculated this cost using directly the great circle distance between two locations) and, in Chapter 3, I assumed equal accessibility for all individuals. However, wind is likely to influence the cost of movement for birds, and to complicate the relationship between distance travelled and energetic cost, in turn affecting the distribution of individuals. Indeed, wind can affect where birds forage (e.g. Weimerskirch et al. 2012), their migration routes (Kranstauber et al. 2015), and even where bird species can/cannot be found (because of their aerodynamic performances, e.g. Suryan et al. 2008).

Revell and Somveille (2017) introduce a mechanistic model that can potentially be useful for better quantifying the cost of travel when studying habitat selection. Their model is inspired by statistical mechanics and relies on simple decision rules based on movement costs (here, influenced by wind strength and direction) and resources (here, modelled using Chlorophyll-a concentration maps). In such framework, it would be possible to model individual paths incorporating more factors than with simple correlative approaches (and potentially identify additional individual differences, e.g. with respect to navigation under different wind conditions).

7.3.2.2.2 Additional potential costs

Although I tried in this thesis to quantify the costs and benefits of movement, there are additional potential costs that might constrain species ranges. Indeed, there can be density-dependent mechanisms related with competition (problematic when there are too many conspecifics in the same area) or the ability to find mates (problematic when there are too few conspecifics in the same area). Such effects could be accounted for, by combining movement data with abundance data (keeping in mind the density-dependent and therefore dynamic nature

of this effect). In particular for North America, such data are increasingly made available by eBird (ebird.org), which uses lists of observations made by the general public and models controlling for various biases inherent to citizen science to generate abundance maps for a wide range of bird species. Although such data are available for terrestrial birds, it would be more complicated for seabirds because birds at sea are rarely observed (apart from at-sea surveys but the spatial coverage of these surveys is low).

7.3.2.3. Causality

Although in this thesis I found a relationship between environmental conditions and geographical space use, I was only able to correlate the two, and not to understand the causal links between them. For the relationship between environmental preferences and site fidelity, see section **Erreur ! Source du renvoi introuvable.**. Similarly, in Chapter 5, I found a trade-off between environmental conditions (climatic niche tracking and amount of resources) and migratory distance: However; I could not distinguish whether the observed patterns result from an active choice or whether environmental conditions encountered are simply a side effect of geographic decisions. Is it because individuals move (for other reasons) that they experience this change in environmental conditions? Or is it because they seek a change in environmental conditions that individuals move?

Whether individuals make decisions based on geography (i.e. site fidelity emerging from, e.g., site familiarity or information from conspecifics), or based on the environment, is likely to influence their response to environmental change or habitat destruction. Indeed, if an area is damaged but what matters is the environmental conditions (and not the specific site), and if there is still some degree of redundancy in environmental conditions, individuals should be able to recover more easily than if it is the geographical location that matters (see sections **Erreur ! Source du renvoi introuvable.** and **Erreur ! Source du renvoi introuvable.**).

7.3.2.4. Difficulties in characterising the environment

A proper characterisation of the environment is necessary for understanding what drives the locations of individuals. The abiotic environment can act (1) as a constraint (e.g. winter harshness for passerines, see Chapters 5 and 6) or (2) as a proxy for the amount of resources (e.g. bathymetry and sea surface temperature acting as proxies for marine waters productivity) or the distribution of a certain type of prey. Often we use environmental variables to get access to information on resources, but the relationship is likely to be indirect and our descriptions unprecise, more so when the studied species are high in the food chain (Grémillet et al. 2008).

It is also particularly complicated to get information on resource types (e.g. in Chapters 5 and 6 of this thesis: although NDVI provides a proxy for the amount of available resources, I am unable to model the types of resources directly), making it impossible to identify individual diet specialisation. Additionally, such environmental proxies might be unsuitable predictors of certain types of resources – mostly anthropogenic resources (e.g. landfill, garden feeding or fisheries discards). However, although more complex an approach, there is scope for a better description of resources, by directly modelling their distribution. For example, (Courbin et al. *in prep*) were able to identify individual specialisation in Scopoli's shearwaters, *Calonectris diomedea*, by modelling the distribution of their prey using at-sea transects and environmental predictors.

7.3.2.5. Additional perspectives

7.3.2.5.1 Importance of environment found on route

Throughout the thesis I focused on locations where birds spend a high amount of time (foraging areas for seabirds, breeding and non-breeding ranges for the migratory passerines). I therefore ignored stopovers sites (for migratory birds), as well as on route locations (transit locations for seabirds, migratory path for migratory passerines). However, the conditions found on route are likely to influence the final destinations (e.g. preventing birds to go to areas with better suited environmental conditions), biasing our understanding of what drives the choice of breeding/non-breeding grounds or foraging areas. Stopover sites have been found to be important in limiting population sizes (through predation, parasitism and competition, Newton 2008), although the effect is likely to be more prevalent for birds whose potential staging areas are spatio-temporally restricted (e.g. swans at their stopover site in the White Sea, feeding on a pondweed that only becomes available as water unfreezes and that becomes available for shorter amounts of time every day as it gets eaten out, Nolet and Drent 1998). At transit locations or along the migratory path, the environmental conditions that are more likely to matter are those related with ease-of-flight, such as wind, but also the presence of major barriers, such as mountains or water bodies. The increasingly available detailed movement data (multiple locations per individual) brings new opportunities for testing whether conditions found on route influence the foraging or seasonal grounds (and therefore our understanding of what affects the choice of these destinations).

7.3.2.5.2 Flexibility

An interesting question that could not be addressed in my thesis is what the degree of flexibility in individual behaviours is. This question is relevant not only regarding individual geographical

space use and strategies (e.g. 'obligate' vs. 'facultative' partial migration) but also regarding their drivers. I could not answer this question because the data I had were either too short-term (only one part of a breeding season for the PPT-tracked albatrosses) or long-term enough but with too few points per individual (ringing data). Longer datasets, with detailed data for multiple seasons per individual, are needed to quantify levels of flexibility. However, such data are not always easy to get. Bird rings, although lasting for the bird's whole life, are not re-sighted often enough for this purpose. Tracking data usually have the opposite problem, as loggers usually do not last long enough (mostly because of battery limitations) to carry out such studies, and it is often not easy to recapture the same birds multiple seasons in a row. However, although characterised by a low spatial and temporal resolution (making it harder to identify individual differences), geolocators have the advantage of having longer-lasting batteries so birds can be tracked for several consecutive years, therefore providing some potential for studies on individual movement and space use flexibility (e.g. Daunt et al. 2014). And more recently, loggers with solar panels (therefore able to work for longer periods of time) and transmitting devices (therefore not requiring the recapture of the bird) have been developed, providing additional potential for such longer-term studies.

See section 7.4 for consequences of these different degrees of flexibility.

7.3.2.5.3 Generality of the studied patterns

Wider-scale studies are needed to understand what happens not only within populations but also between populations. Such studies could address (1) whether different populations of the same species specialise on the same resources, and (2) whether, within these populations (potentially exposed to different environmental conditions), the levels of individual specialisation (or site fidelity) are the same. Additionally, comparisons between populations that are more or less further apart geographically or more or less genetically differentiated. Although some studies have attempted to address (1) (e.g. Wakefield et al. 2011), it can be complicated, as different populations are likely to be exposed to different resources and habitats. However, the approach presented in (Matthiopoulos et al. 2011) (Generalised Functional Responses) would allow taking these differences in habitat availability and accessibility into account.

Regarding (2), the analysis in Chapter 3 provides a comparison between the level of individual specialisation in Black-browed albatrosses in South Georgia (Chapter 3) and in Kerguelen (Patrick and Weimerskirch 2017). See Chapter 3 for a discussion on potential explanations for these differences. The drawback of this comparison is that the data types and methodologies

differ between the two studies. In general, a unified framework to quantify individual specialisation would be very useful to allow comparisons across studies.

7.3.2.5.4 Predictability

Another interesting question that could not be addressed in this thesis is whether we can predict under which circumstances there should be individual specialisation (i.e. when it would pay for individuals to be specialised). Individual specialisation should be more advantageous when the environment is more predictable (see Wakefield et al. 2015, Phillips et al. 2017). Population density is also likely to play a role, through competition pressure (Araújo et al. 2011). Similarly, if resources are abundant, competition is likely to be weaker, therefore reducing the benefits of individual specialisation. To test these hypotheses, longitudinal studies would be useful, contrasting the degree of individual specialisation between years with different environmental conditions (e.g. different prey abundances). Comparisons between populations would also be informative, for example between small and big populations, to test for the effect of population density on the incidence and intensity of individual specialisation.

7.4. Implications

7.4.1. Population/species characterisation

The degree of individual differences, both in geographical and in environmental space use, influences which sample sizes are needed to obtain a representative view of the whole population. Indeed, if there is spatial segregation, more individuals will need to be sampled to understand the species/population's spatial distribution than if all use the same area. Similarly in environmental space, if there is individual specialisation, more individuals will need to be sampled to understand the full range of preferences of the species.

In a context of limited monitoring resources, it is pertinent to ask whether we should sample more individuals for a shorter period of time, or the opposite. Because individual albatrosses tend to be generalists, the results in Chapter 3 suggest that resources would be better targeted at better understanding where individuals go and which environment they select rather than doing short-term studies on many more individuals. In contrast, Wakefield et al. (2015) found that northern gannets *Morus bassanus* were highly site faithful. They therefore suggested that, in their case, resources would be better used for tracking many individuals for short periods of time in order to know the areas used by the population. In general, though, it is hard to make recommendations before having already tracked individuals (but see section **Erreur ! Source**

du renvoi introuvable. and the approach in Clay et al. (*in prep*) which at least could provide information on whether or not more sampling is required).

7.4.2. Biological processes

The degree of within-species differences in both geographical and environmental space use is likely to influence biological processes (see Chapter 1 of this thesis) – both in terms of ecological interactions, and in terms of evolutionary processes. For example, the spatial redistribution of individuals from the breeding to the non-breeding range will influence the potential for disease transmission (Webster et al. 2002). Indeed, if populations remain segregated from one season to the next, diseases are less likely to transmit between populations than if individuals randomly redistribute throughout the range.

Regarding fitness consequences of such individual differences, conflicting results have been found in various studies (see Phillips et al. 2017 for a review). Some studies found fitness advantages of a specialised diet (e.g. specialists pigeon guillemots *Cepphus Columba* fledged more chicks than generalists, Golet et al. 2000) but others did not (e.g. in Brunnich guillemots *Uria lomvia*, Woo et al. 2008). Patrick and Weimerskirch (2017) found that habitat specialisation did not have an effect on the reproductive success of black-browed albatrosses *Thalassarche melanophrys*. Similarly, in terms of site fidelity, results were also variable, with site-faithful female black browed albatrosses having a higher reproductive success (Patrick and Weimerskirch 2017) but no effect being found in European shags *Phalacrocorax aristotelis* (Daunt et al. 2014).

Note that all of these studies were carried out at the individual level, but it would also be interesting to compare populations characterised by higher or lower levels of individual specialisation, in terms of population growth rate. This would also require a unified framework for quantifying individual specialisation, which would allow making comparisons.

7.4.3. Conservation implications

7.4.3.1. Spatial planning

Intraspecific patterns of geographical space use influence the choice of areas to prioritise for conservation. For example, knowing how migratory individuals redistribute from one season to the next within their species' range can guide conservation efforts towards areas that allow

better probabilities of success. Additionally, if individuals redistribute randomly within their range between seasons, the effect of habitat protection or destruction in one subpart of one of the ranges will be more diffuse than if migratory connectivity is very high (see discussion in Chapter 4 of this thesis).

Consistent within-species differences in environmental space use have an influence on the best approach to protect populations. Indeed, if individuals vary in their environmental preferences, areas with a range of various environmental conditions should be targeted by conservation efforts. Phillips et al. (2017) argue that population-level approaches may fail to target important areas, which, although being used by a relatively low proportion of specialised individuals, would buffer the population-levels impacts from anthropogenic impacts, e.g. destruction of habitats, fisheries bycatch or pollutants in areas used by the majority of individuals.

However, although difficult to quantify, the degree of flexibility (see section **Erreur ! Source du renvoi introuvable.**) can also be important to consider when designing protected areas. Indeed, if individuals are not flexible in their preferences, then selecting areas that do not cover the whole range of preferences existing in the population is likely not to be very efficient for protecting species. Phillips et al. (2017) present a comparison of two situations. Some northern gannets show long-term specialisation on fisheries bycatch (Patrick et al. 2015), whereas specialisation on fisheries waste by black-browed albatrosses did not persist from one year to the next (Granadeiro et al. 2011, 2014). For the former, the threat of bycatch only concerns a particular group of individuals specialised on fisheries waste, whereas for the latter, the threat is more diffuse but will constantly be present for the population (as individuals change their foraging strategies with time).

7.4.3.2. Making predictions

7.4.3.2.1 Drivers of spatial differences

Environmental conditions are changing (e.g. global warming, Pachauri et al. 2015). Additionally, anthropisation is increasing, with humans affecting the distribution of resources (see Oro et al. 2013 for a review of human-provided food subsidies). Global change is therefore likely to affect individual decisions and spatial distributions. For example, garden feeding can influence migratory routes (Plummer et al. 2015) and the change in abundance and predictability of resources have been found to affect the decision of whether or not to migrate (e.g. storks feeding on garbage and becoming resident in increasing numbers, Gilbert et al. 2016).

In Chapter 6, although I was not able to test for any dynamic effect (i.e. for any change through time), I found results emphasizing the importance of human population density on the decision of birds to migrate vs. to remain resident, which raised the question of the consequences of future increased urbanisation.

We can also wonder whether global change can influence the incidence of individual specialisation. Indeed, some changes could create additional scope for specialisation by providing extra resources (e.g. seabirds specialising on fisheries discards, Granadeiro et al. 2014), but the effects might be more complex, as anthropogenic sources of food can differ from non-anthropogenic ones as they tend to be more abundant and easily accessible. To my knowledge, no study to date has investigated these effects.

7.4.3.2.2 Consequences of individual differences in environmental preferences

Individual differences in environmental preferences challenge our ability to make predictions about the species' space use. Indeed, the assumption that all individuals of a species have the same environmental preferences and that their preferences are conserved in time underlies species distribution models. However, if there is within-species variation in environmental preferences and if this is not taken into account, predictions based on certain individuals might not reflect the distribution of the whole species.

Additionally, in the future, populations lacking variability are likely to be at a disadvantage if their common resource or habitat is destroyed. Similarly, the time scale of specialisation (see section **Erreur ! Source du renvoi introuvable.**) is also likely to influence the response of populations to environmental changes (Nussey et al. 2007). Hence, to understand the potential for populations to be resilient to environmental change, long-term data on the same individuals ('longitudinal data') are necessary (e.g. Daunt et al. 2014).

7.5. General perspectives

Results in this thesis highlight the importance of not treating species as a block, but rather of considering intraspecific variation. Although this thesis focused on space use, it fits in a more general trend to realise that such intraspecific variation matters (Araújo et al. 2011, Bolnick et al. 2011, Violle et al. 2012). Although with the data I had I could not always investigate this aspect, I argued throughout this Discussion chapter that what ultimately matters is to understand levels of individual consistency. Some authors have even argued that between-individual variation in individual consistency is also highly relevant (Cleasby et al. 2015). There is

therefore a need for tracking data on many more individuals, to overcome the limitations of both datasets used in this thesis (small number of individuals, and small number of observations per individual).

Such data are becoming increasingly available. However, as in all research fields, the increasing availability of data has to be accompanied by the development of appropriate statistical methods to analyse them. A striking example is the case of habitat suitability models: as more data become available, it becomes more and more likely to identify significant variables with traditional modelling methods. However, despite highly significant results (i.e. very small p-values), the percentage of variance explained by such models – if at all reported – is often very limited (e.g. Awkerman et al. 2005), questioning the relevance of these variables for explaining the space use of individuals/species.

Another challenge is to be able to include the identified variation in predictive models. The studies accounting for individual variation nowadays tend to do so by building habitat selection models using mixed models with individual as a random effect (e.g. Wakefield et al. 2011). Predictions are then made by taking the population average (i.e. only the fixed effects). However, I argued in section 7.4 that individual variability can actually matter. The development of methods of predictions able to take this variability into account is therefore necessary.

Overall, thanks to increasing data and new methods, there is a promising research field emerging, with important implications for our understanding of ecological and evolutionary processes, as well as for conservation decisions.

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Žydelis, R., R. L. Lewison, S. A. Shaffer, J. E. Moore, A. M. Boustany, J. J. Roberts, M. Sims, D. C. Dunn, B. D. Best, Y. Tremblay, M. A. Kappes, P. N. Halpin, D. P. Costa, and L. B. Crowder. 2011. Dynamic habitat models: Using telemetry data to project fisheries bycatch. Proceedings of the Royal Society B: Biological Sciences 278:3191–3200.

9. Appendices

9.1. Appendix A – supplementary material for Chapter 3

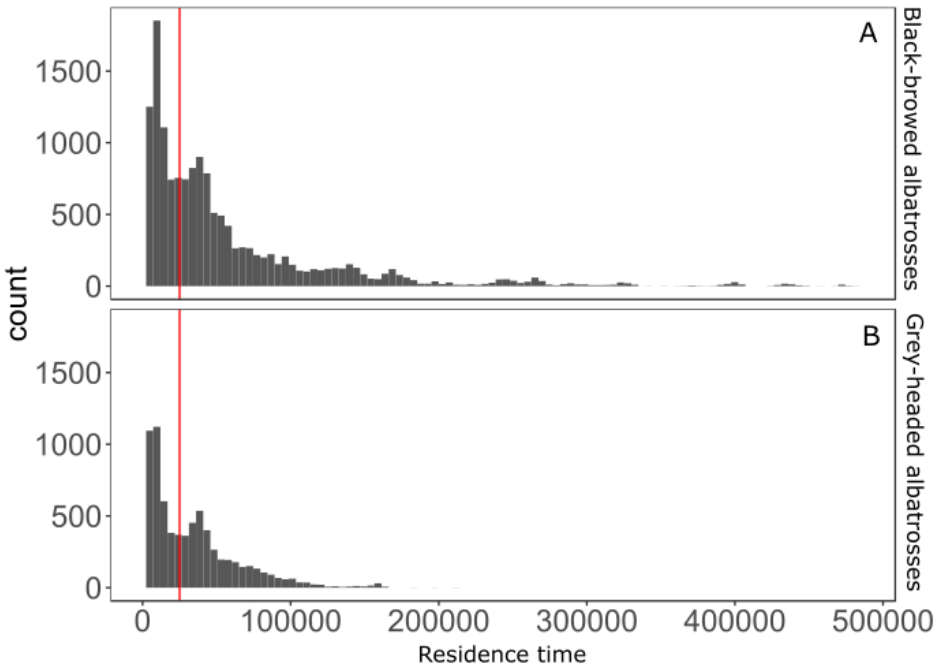

Figure A1: Distribution of residence times for A) black-browed albatrosses, B) grey-headed albatrosses tracked from South Georgia during chick-rearing. Vertical red line: selected threshold value for the selection of locations for the analyses.

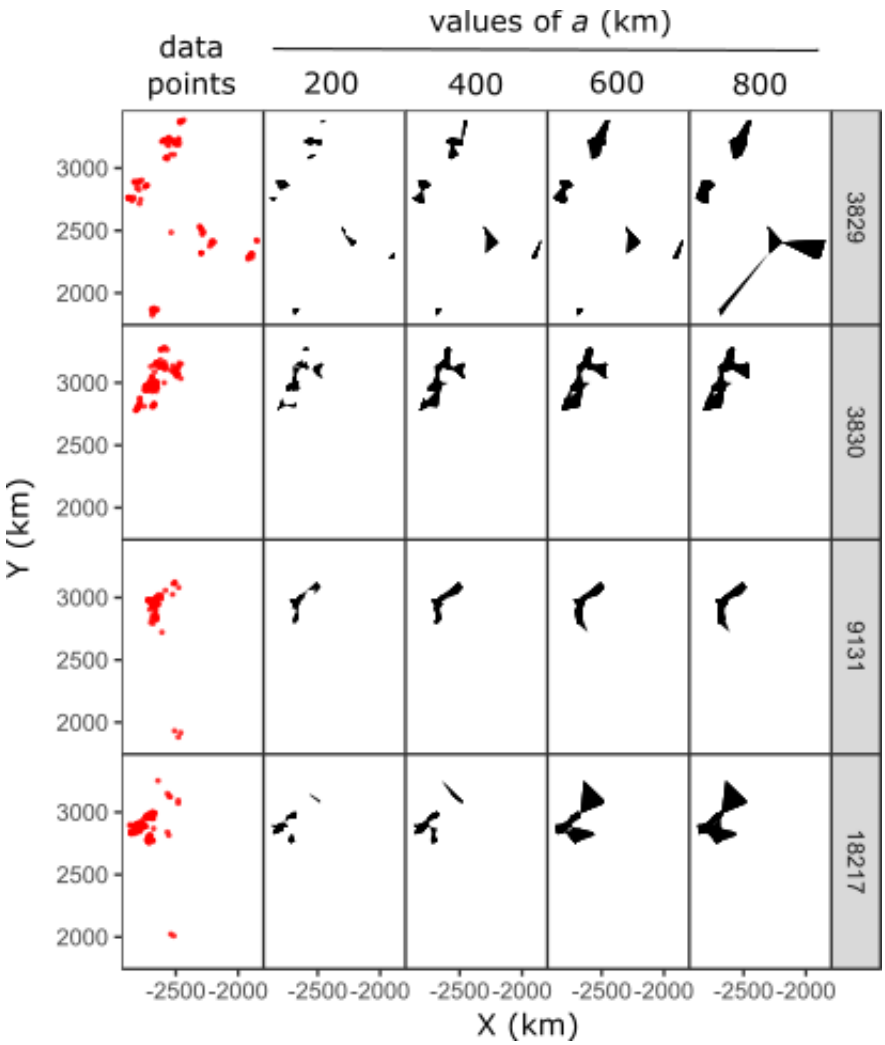

Figure A2: Effects of different values for parameter a on the resulting hypervolumes in geographical space for black-browed albatrosses.

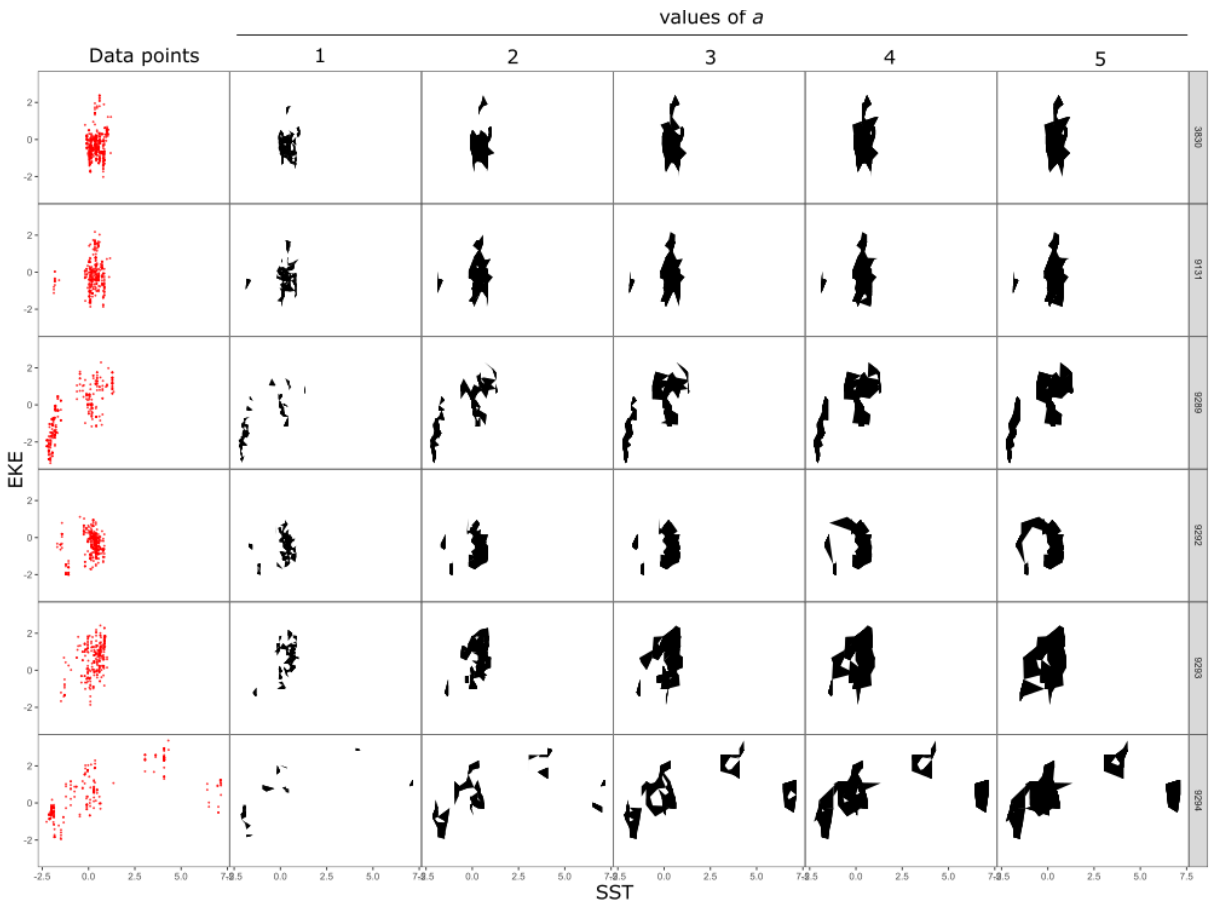

Figure A3: Effects of different values for parameter a on the resulting hypervolumes in environmental space for black-browed albatrosses, projecting in the EKE-SST plane.

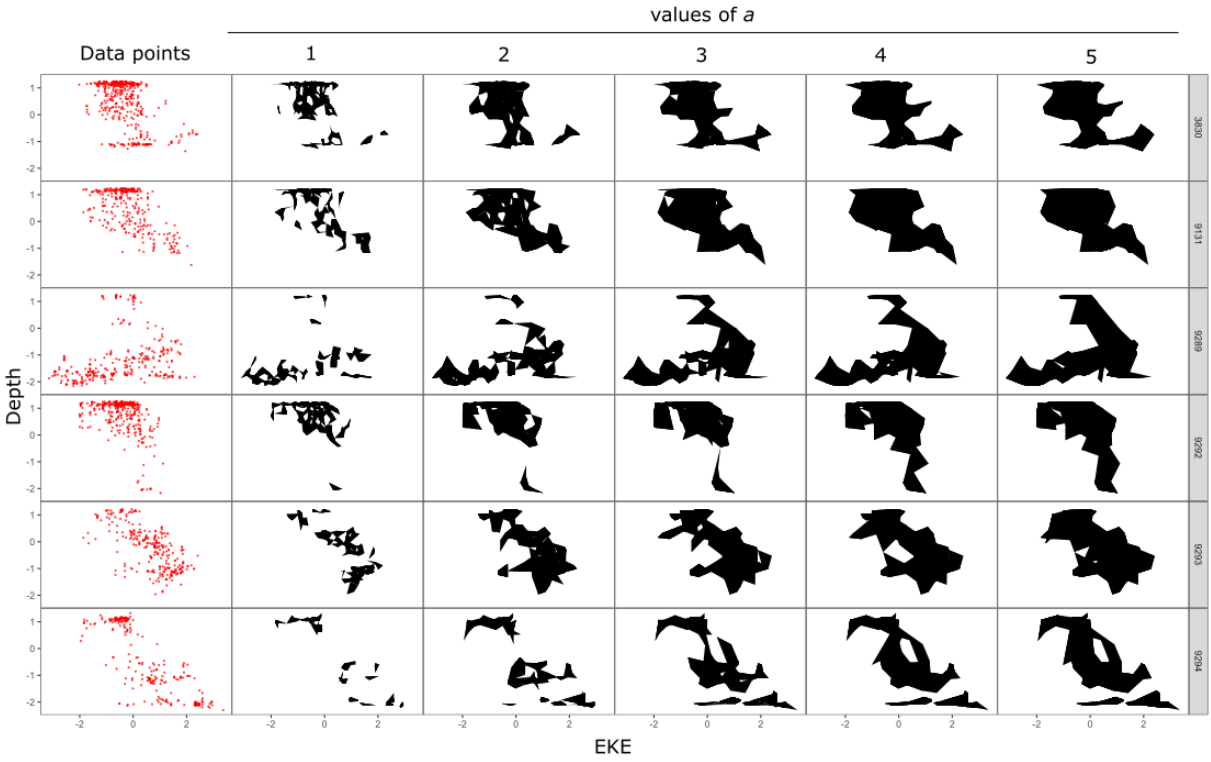

Figure A4: Effects of different values for parameter a on the resulting hypervolumes in environmental space for black-browed albatrosses, projecting in the EKE-depth plane.

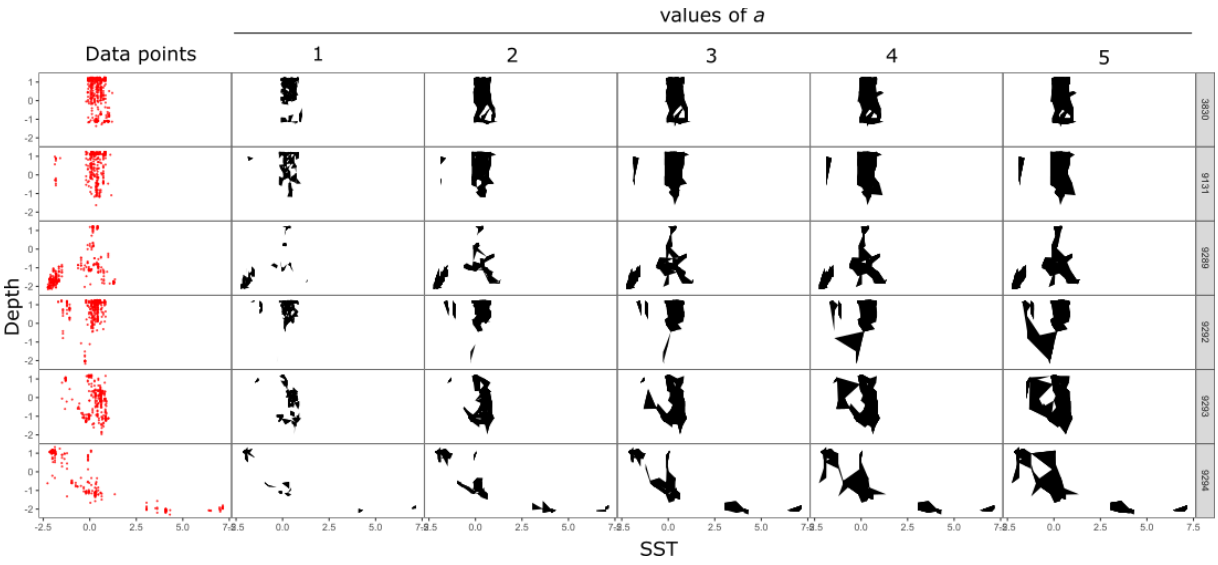

Figure A5: Effects of different values for parameter a on the resulting hypervolumes in environmental space for black-browed albatrosses, projecting in the SST-depth plane.

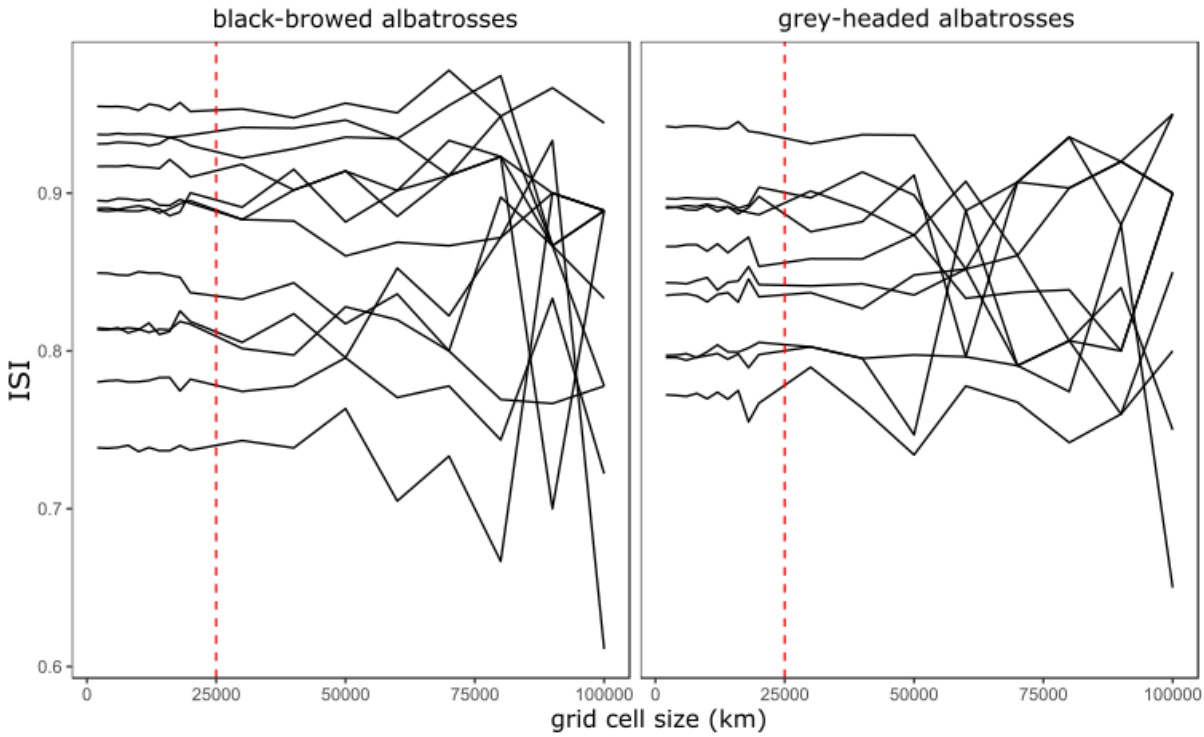

Figure A6: Effect of different grid cell sizes on the resulting individual specialisation index (ISI) in geographical space. Red dotted line: grid cell size used for the analysis.

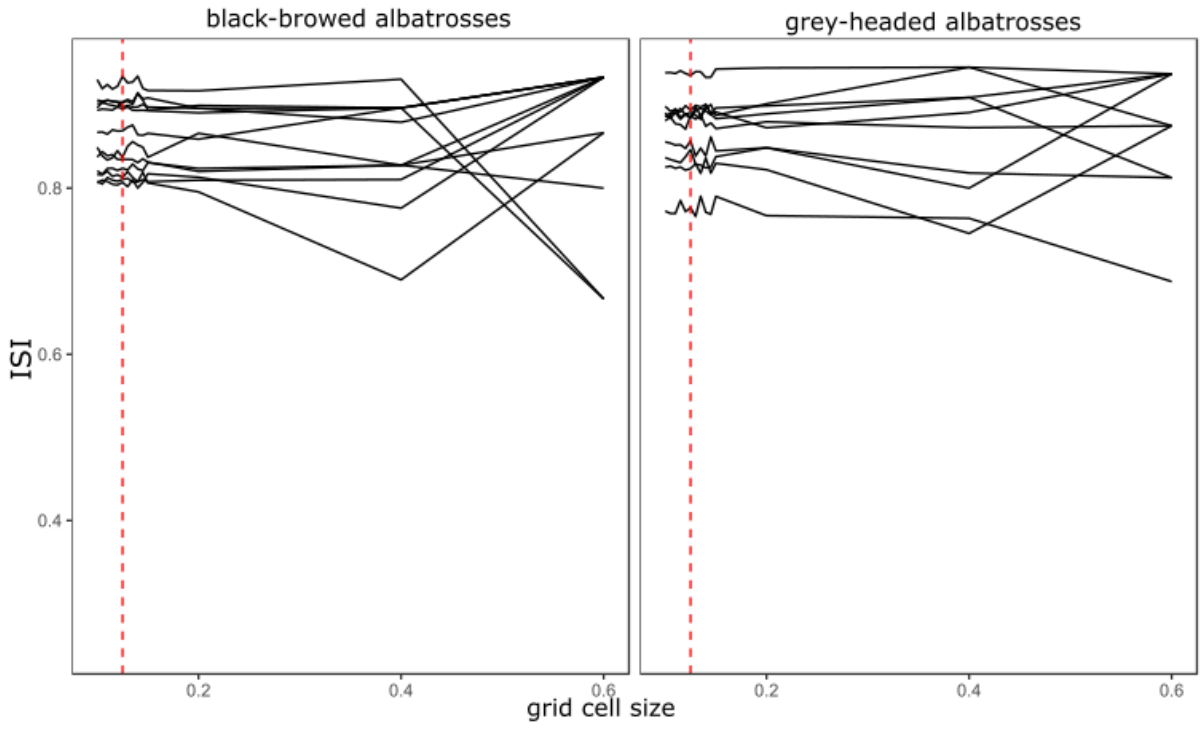

Figure A7: Effect of different grid cell sizes on the resulting individual specialisation index (ISI) in environmental space. Red dotted line: grid cell size used for the analysis.

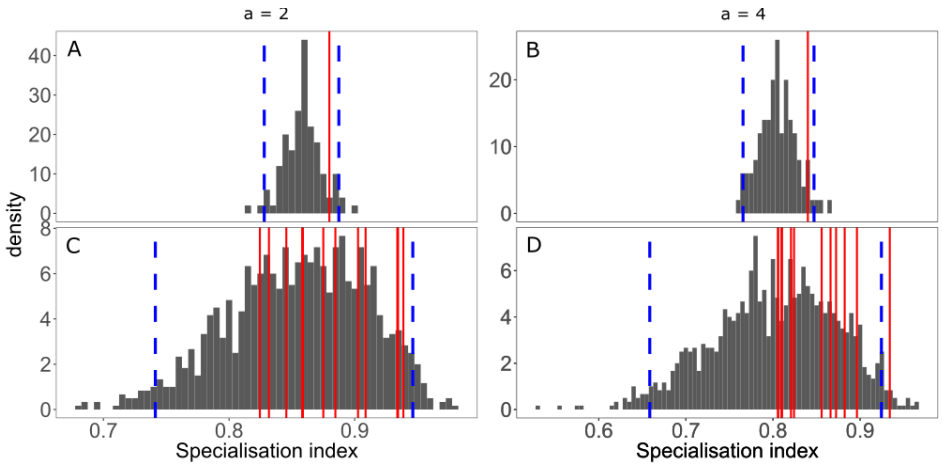

Figure A8: Effect of values for parameter a on ISI values: comparison between the null model (histogram; vertical blue dotted lines: 95% CI) and the empirical values (vertical red lines), in three-dimensional environmental space for black-browed albatrosses: A) median population values for a = 2; B) median population values for a = 4; C) individual values for a = 2; D) individual values for a = 4.

PTT	Start date	End date	Number of locations	Sex
3829	01/03/2002	26/02/2002	265	F
3830	01/02/2002	31/01/2002	475	F
9131	01/02/2002	31/01/2002	322	F
9289	01/03/2002	28/03/2002	311	F
9292	01/02/2002	31/01/2002	378	M
9293	01/03/2002	28/02/2002	285	M
9294	01/03/2002	28/02/2002	286	F
14406	01/02/2002	31/01/2002	413	M
14409	01/02/2002	31/01/2002	466	M
17987	01/03/2002	28/02/2002	349	F
17988	01/03/2002	28/02/2002	337	M
18217	01/03/2002	28/02/2002	356	M

Table A1: Summary of the tracking dataset used for Black-browed albatrosses (after selection of foraging locations using residence time and daytime locations only).

PTT	Start date	End date	Number of locations	Sex
3829	05/02/2001	27/02/2001	151	F
3830	01/03/2001	28/02/2001	153	M
9131	01/03/2001	28/02/2001	141	M
9132	01/03/2001	28/02/2001	168	F
9287	01/03/2001	27/02/2001	147	F
9289	02/03/2001	28/02/2001	150	F
9292	01/03/2001	28/02/2001	165	M
9293	01/03/2001	28/02/2001	151	F
9294	01/03/2001	28/02/2001	231	M
22955	05/02/2001	16/02/2001	50	M

Table A2: Summary of the tracking dataset used for Grey-headed albatrosses (after selection of foraging locations using residence time and daytime locations only).

9.2. Appendix B – supplementary material for Chapter 4

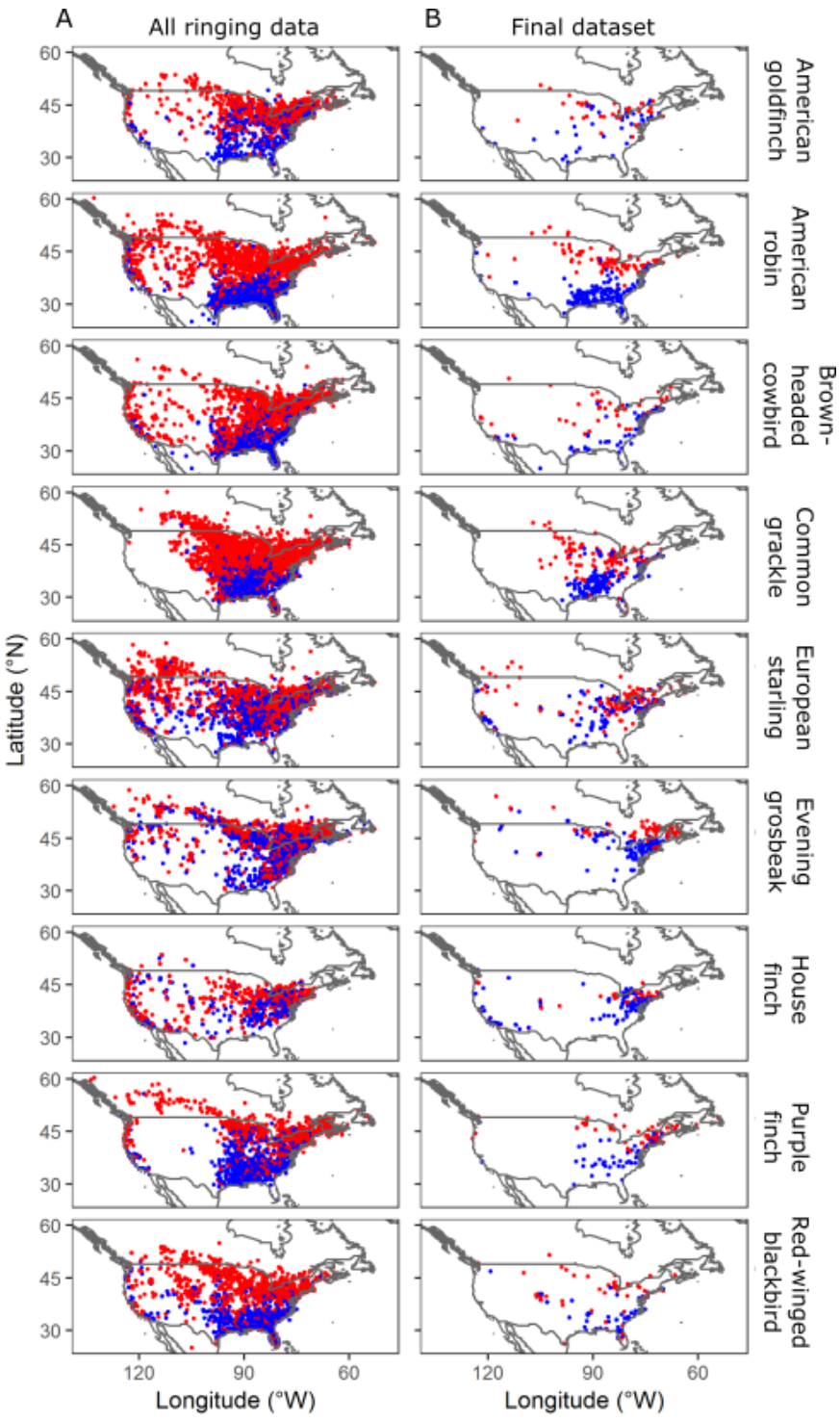

Figure B1: Comparison between the whole ringing dataset (A) and the final dataset (B) for the 9 selected species. Most areas of presence are represented in the final dataset, except from areas in the far north-west that are occupied in winter by American goldfinches, House finches or Purple finches; as well as areas in the central part of the US for American robins.

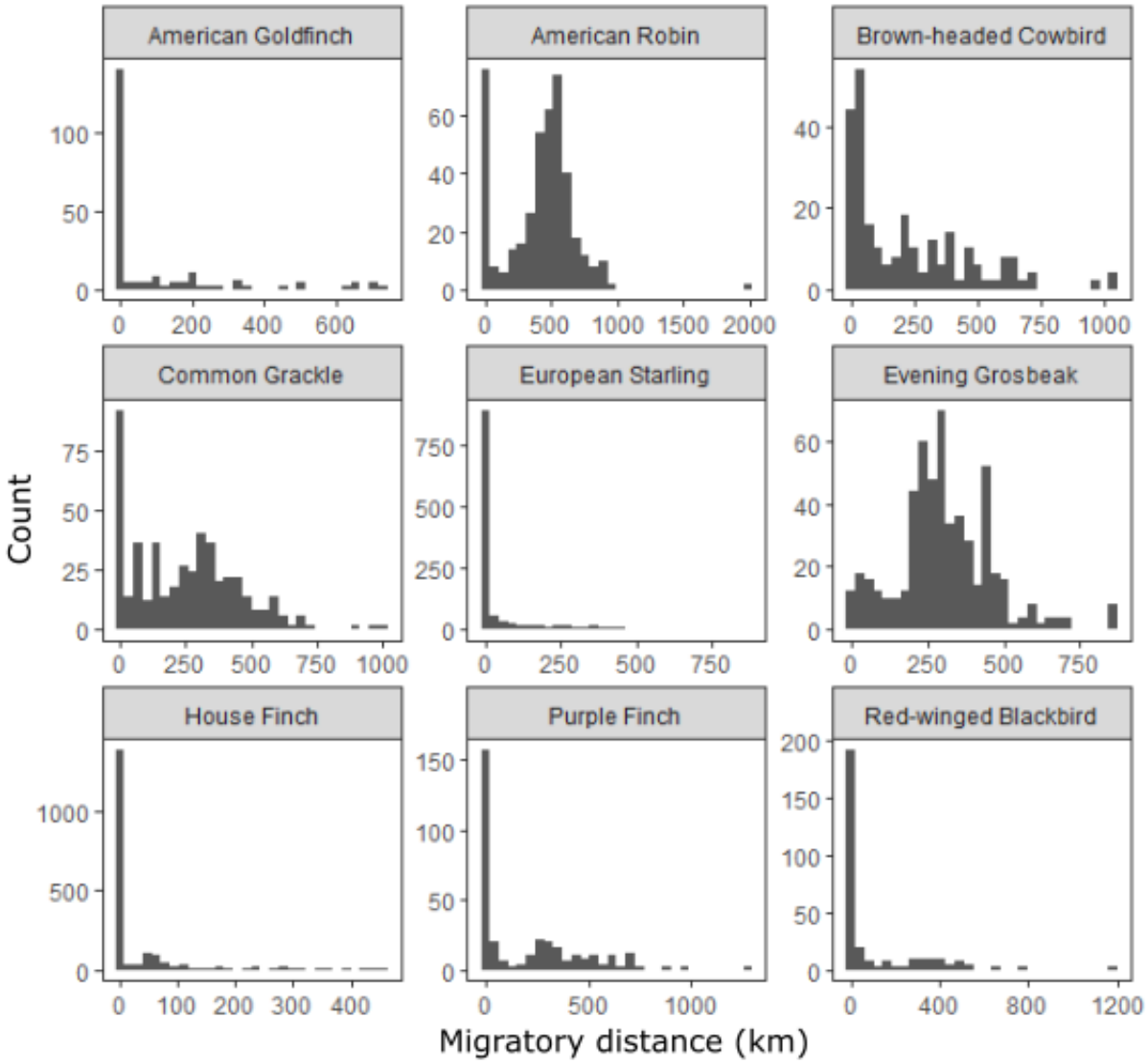

Figure B2: Histograms of migratory distances for each species.

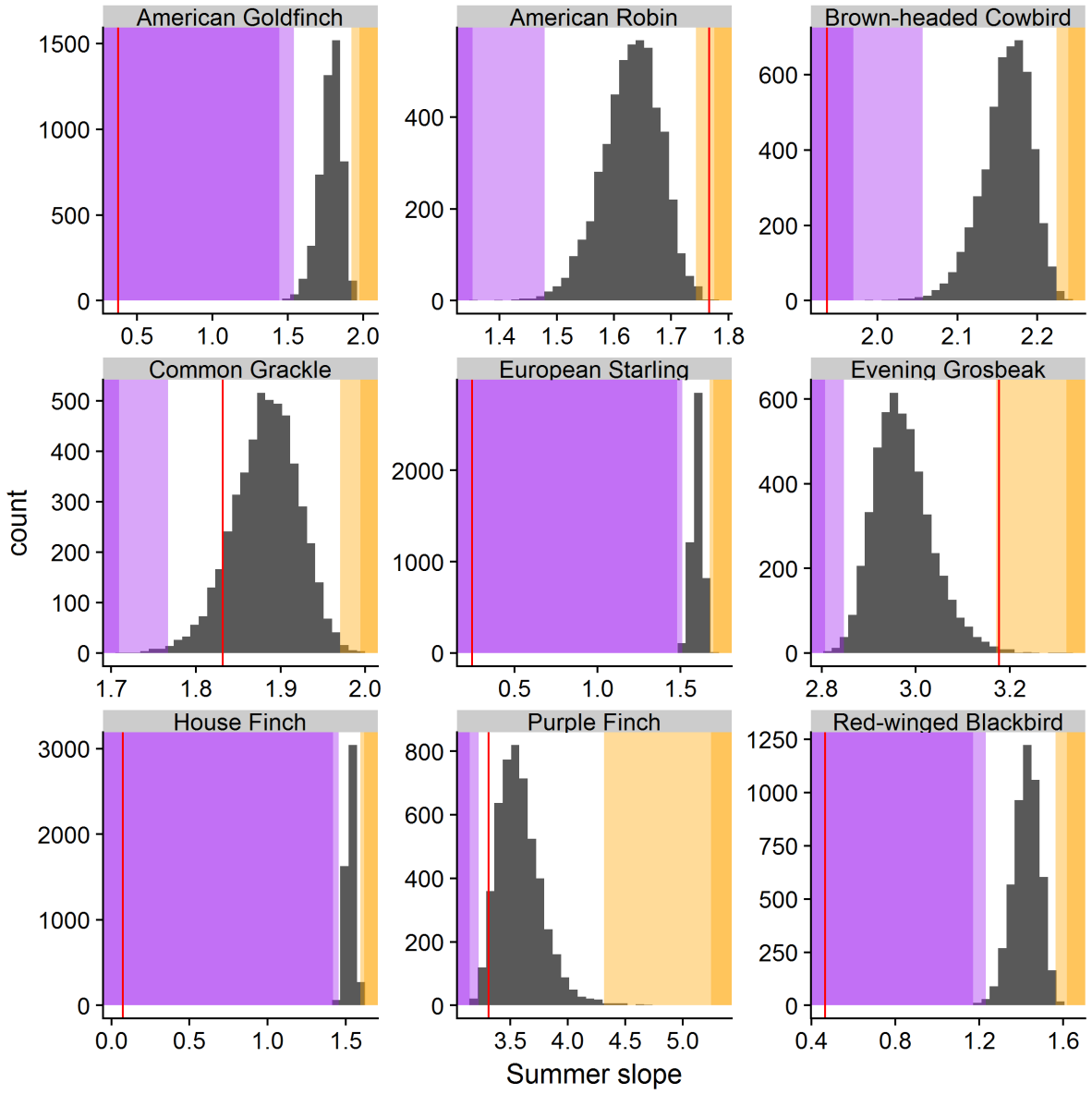

Figure B3: Null distributions of summer slopes for test 2, when data contains all individuals. Histogram: distribution of the values from the randomisation. Dark purple and dark orange: outside of the 99% confidence interval; light purple and light orange: outside of the 95% confidence interval; purple: more chain-like than random, orange: more leapfrog-like than random. Red vertical line: empirical summer slope for test 2.

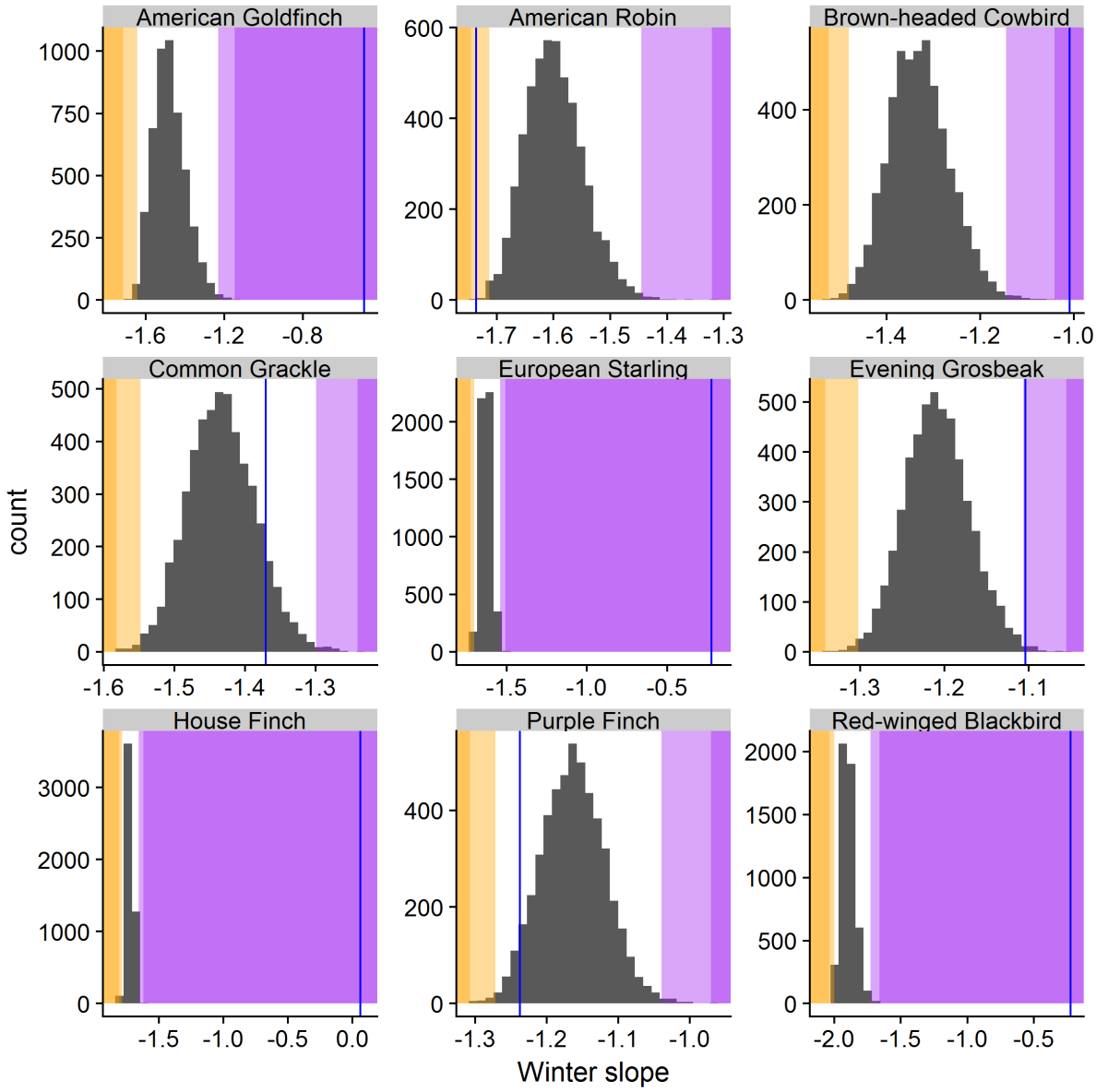

Figure B4: Null distributions of winter slopes for test 2, when data contains all individuals. Histogram: distribution of the values from the randomisation. Dark purple and dark orange: outside of the 99% confidence interval; light purple and light orange: outside of the 95% confidence interval; purple: more chain-like than random, orange: more leapfrog-like than random. Blue vertical line: empirical winter slope for test 2.

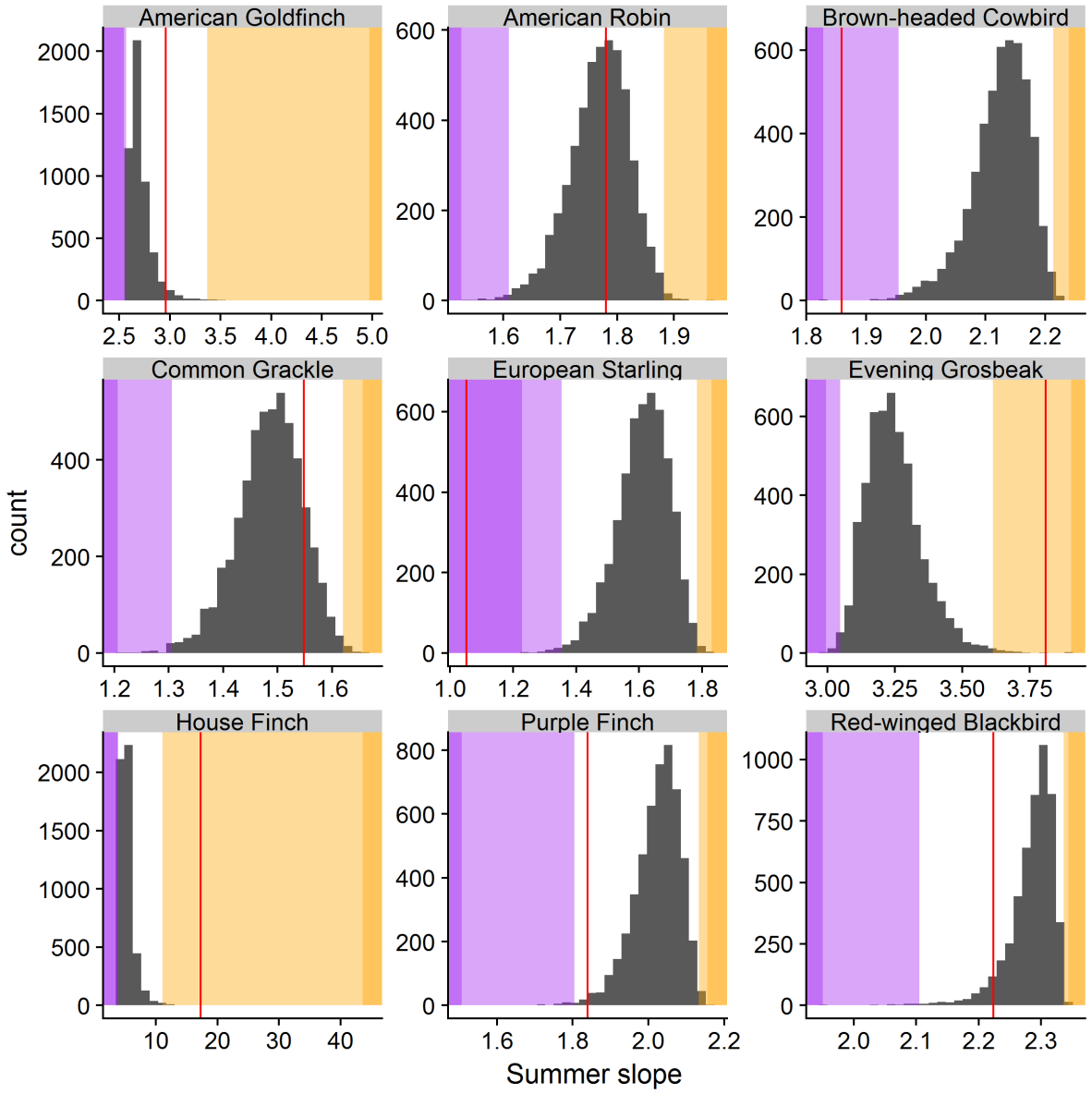

Figure B5: Null distributions of summer slopes for test 2, when data contains only migratory individuals. Legend as in Figure B3.

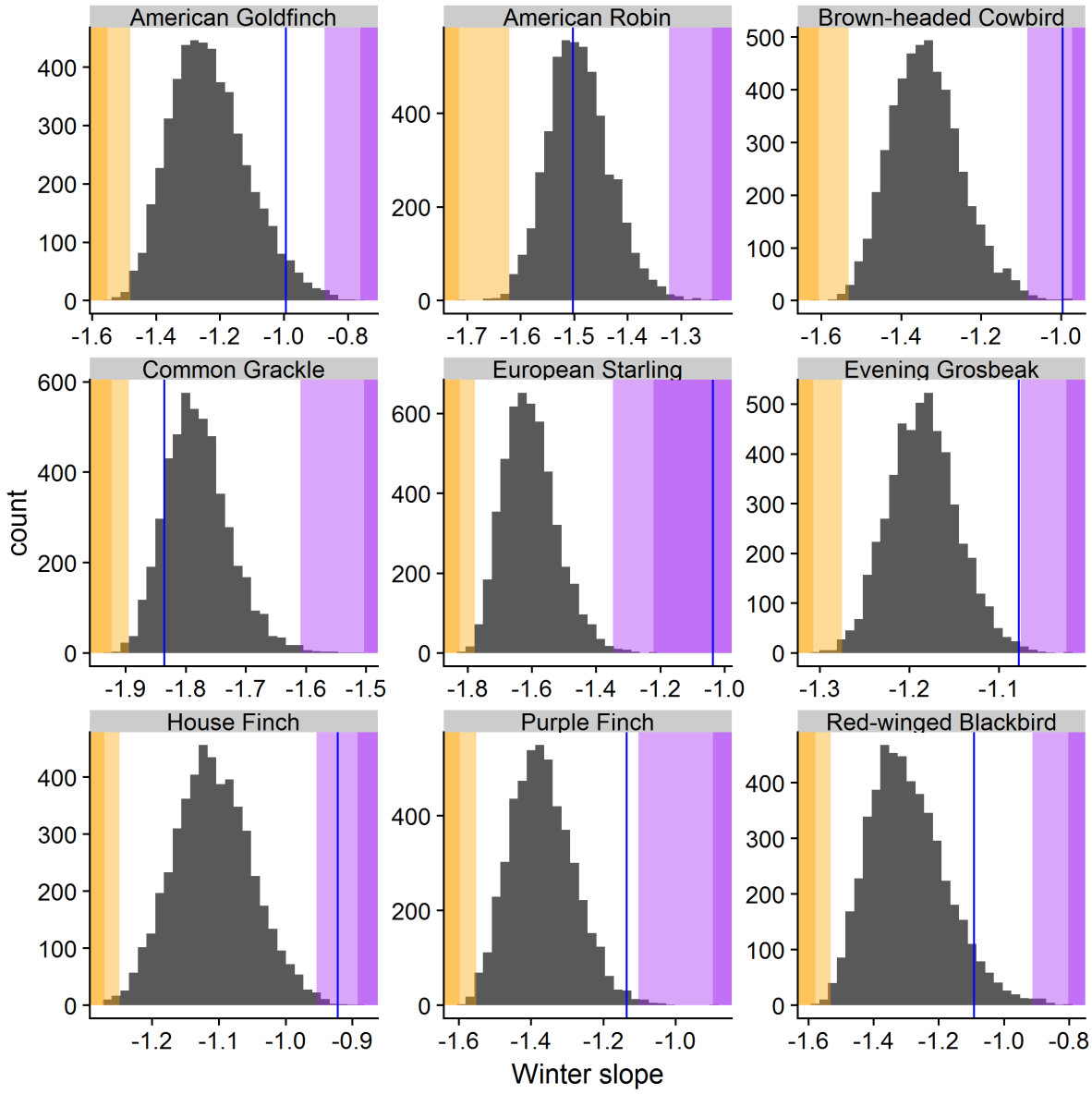

Figure B6: Null distributions of winter slopes for test 2, when data contains only migratory individuals. Legend as in Figure B3.

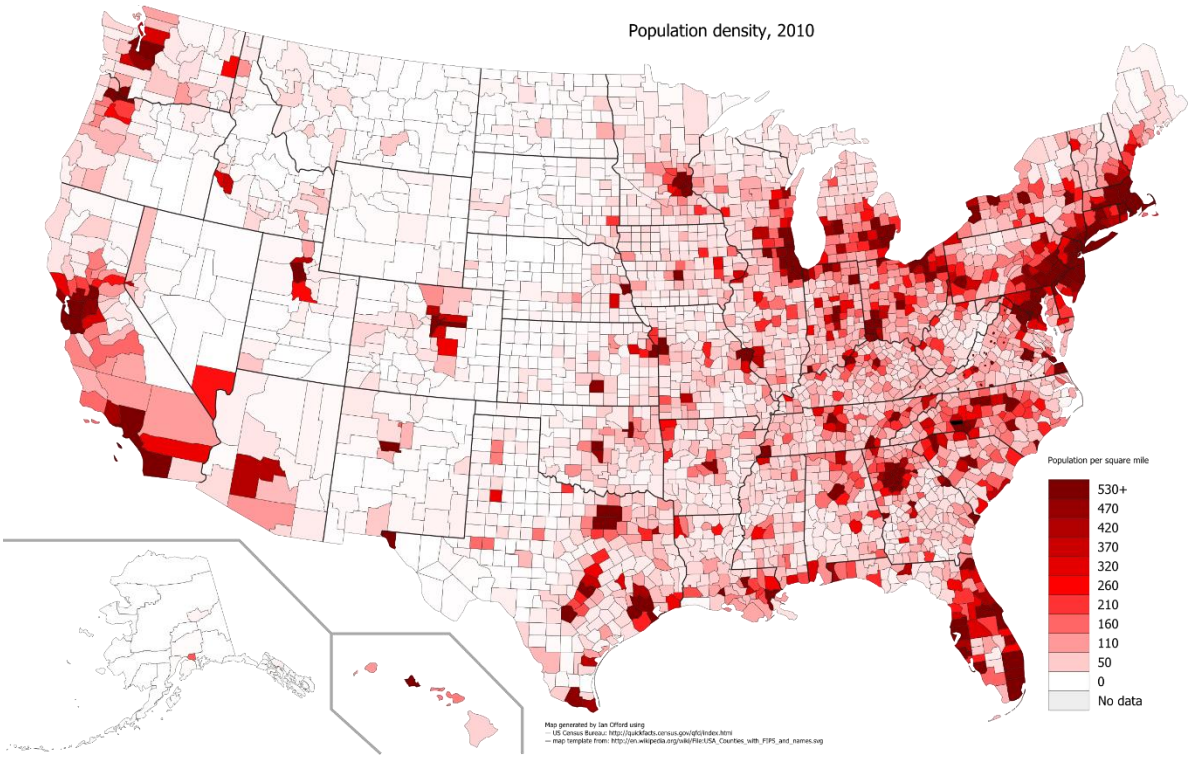

Figure B7: Distribution of human population density in the United States. Source: http://ecpmlangues.u-strasbg.fr/civilization/geography/maps

9.4. Appendix C – supplementary material for Chapter 5

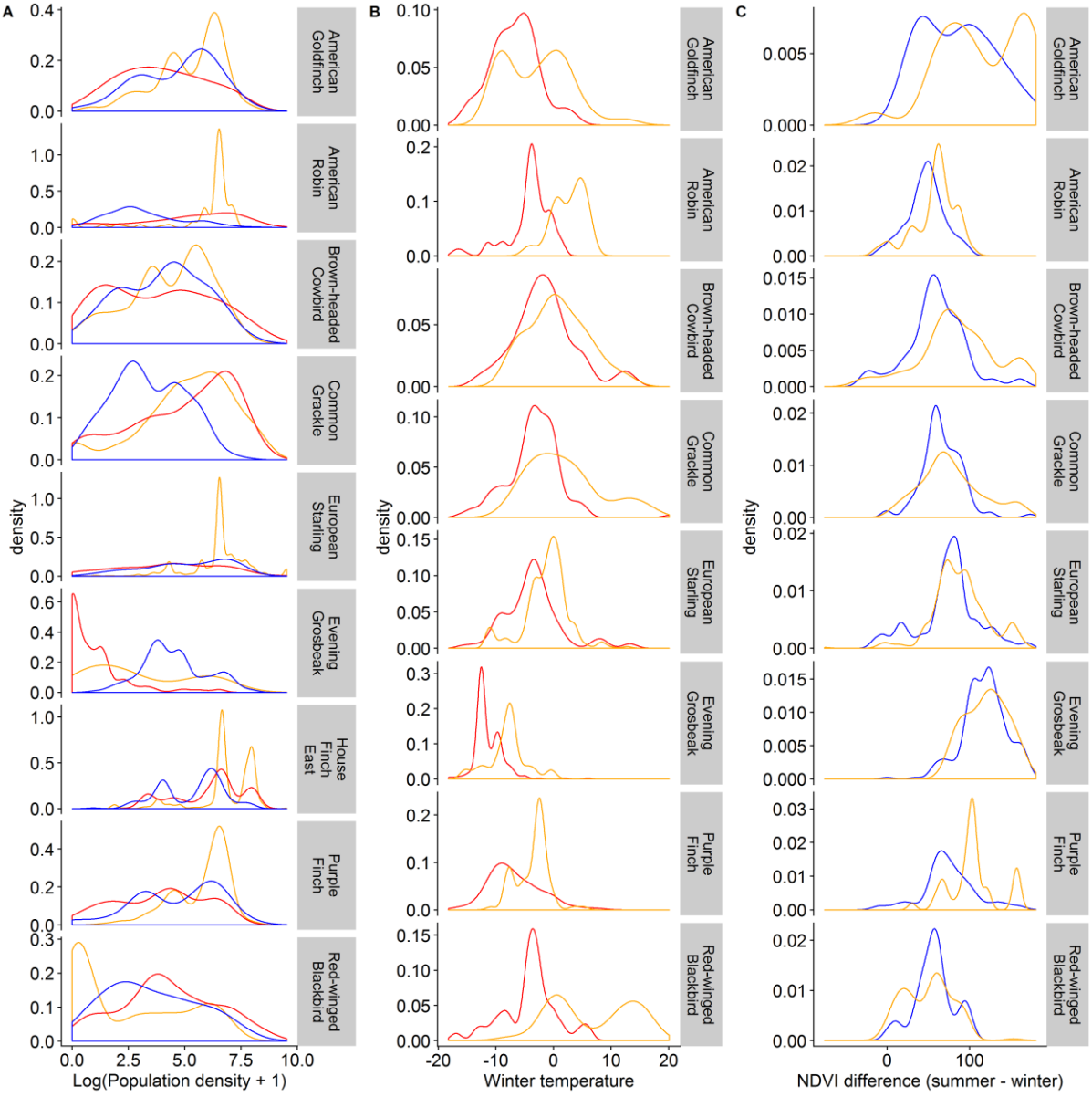

Figure C1: Distribution of sightings of summer migrants (red), winter migrants (blue) and residents (orange) for different values of log(Human population density + 1), winter temperature, and NDVI summer surplus ($NDVI_{summer} - NDVI_{winter}$) at the corresponding locations.

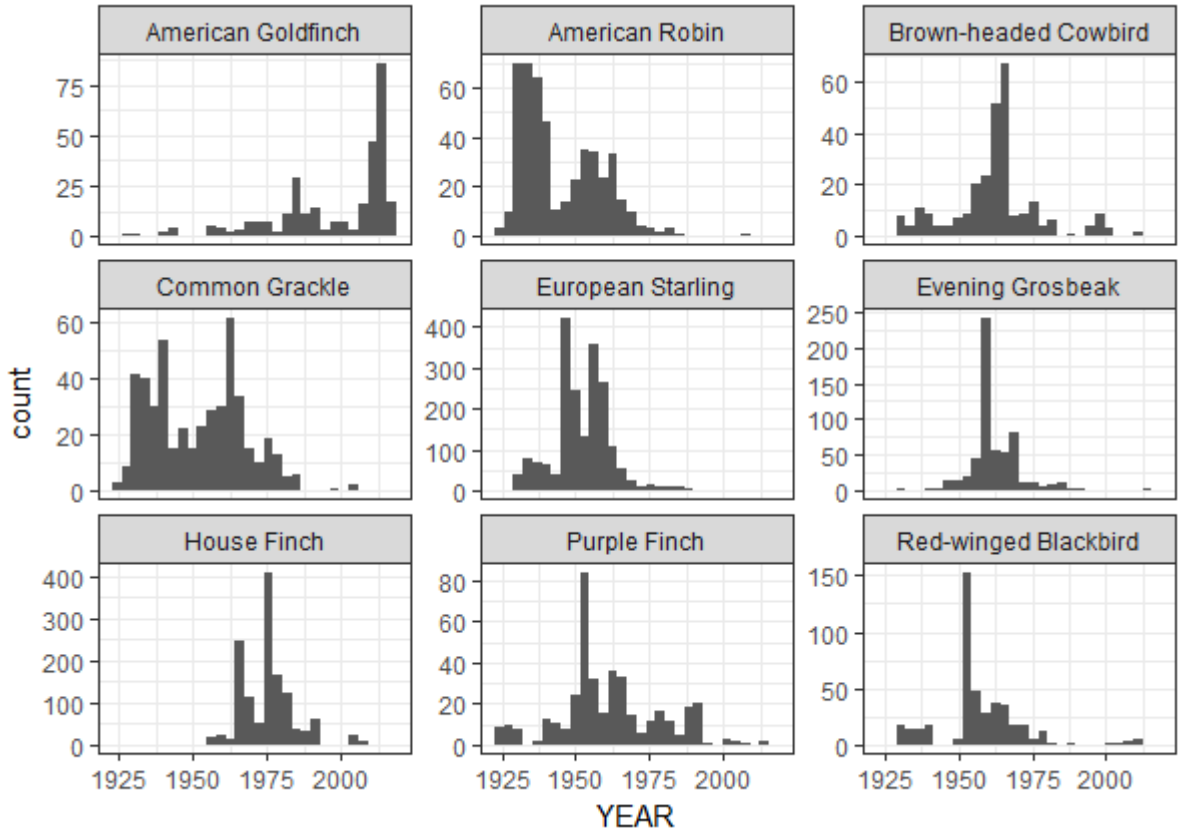

Figure C2: Temporal distribution of ringing / re-sighting events for each species. House finch records correspond to only the Eastern population (East of 95˚W)